This is a digital copy of a book that was preserved for generations on library shelves before it was carefully scanned by Google as part of a project to make the world's books discoverable online.

It has survived long enough for the copyright to expire and the book to enter the public domain. A public domain book is one that was never subject to copyright or whose legal copyright term has expired. Whether a book is in the public domain may vary country to country. Public domain books are our gateways to the past, representing a wealth of history, culture and knowledge that's often difficult to discover.

Marks, notations and other marginalia present in the original volume will appear in this file - a reminder of this book's long journey from the publisher to a library and finally to you.

Usage guidelines

Google is proud to partner with libraries to digitize public domain materials and make them widely accessible. Public domain books belong to the public and we are merely their custodians. Nevertheless, this work is expensive, so in order to keep providing this resource, we have taken steps to prevent abuse by commercial parties, including placing technical restrictions on automated querying.

We also ask that you:

+ *Make non-commercial use of the files* We designed Google Book Search for use by individuals, and we request that you use these files for personal, non-commercial purposes.

+ *Refrain from automated querying* Do not send automated queries of any sort to Google's system: If you are conducting research on machine translation, optical character recognition or other areas where access to a large amount of text is helpful, please contact us. We encourage the use of public domain materials for these purposes and may be able to help.

+ *Maintain attribution* The Google "watermark" you see on each file is essential for informing people about this project and helping them find additional materials through Google Book Search. Please do not remove it.

+ *Keep it legal* Whatever your use, remember that you are responsible for ensuring that what you are doing is legal. Do not assume that just because we believe a book is in the public domain for users in the United States, that the work is also in the public domain for users in other countries. Whether a book is still in copyright varies from country to country, and we can't offer guidance on whether any specific use of any specific book is allowed. Please do not assume that a book's appearance in Google Book Search means it can be used in any manner anywhere in the world. Copyright infringement liability can be quite severe.

About Google Book Search

Google's mission is to organize the world's information and to make it universally accessible and useful. Google Book Search helps readers discover the world's books while helping authors and publishers reach new audiences. You can search through the full text of this book on the web at `http://books.google.com/`

SCIENCE LIBRARY
QL
950.5
.H65

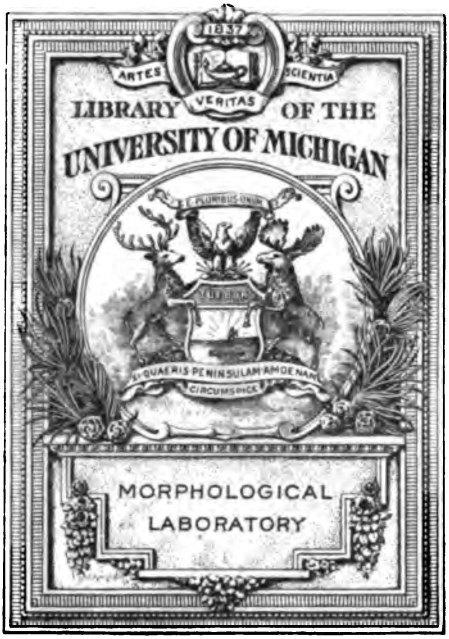
BUHR B
a39015 00004812 7b

Developmental History
of
Primary Segments of the Vertebrate Head.

A Thesis
for the
Degree of Doctor of Philosophy
presented from the
Department of Zoology
to the
Faculty of the College of Liberal Arts
of
Northwestern University.
June, 1899
by
Charles Hill.

With 3 plates and 4 figures in text.

Jena,
Gustav Fischer
1900.



LIBRARY OF THE
UNIVERSITY OF MICHIGAN

MORPHOLOGICAL
LABORATORY

SCIEN LIBRARY
QL
950.5
.H65

Orig covers
Gr.

Developmental History
of
Primary Segments of the Vertebrate Head.

1191..3

A Thesis
for the
Degree of Doctor of Philosophy
presented from the
Department of Zoology
to the
Faculty of the College of Liberal Arts
of
Northwestern University.
June, 1899
by
Charles Hill.

With 3 plates and 4 figures in text.

Jena,
Gustav Fischer
1900.

Abdruck
aus den
Zoologischen Jahrbüchern,
Abtheilung für Anatomie und Ontogenie der Thiere.
Herausgegeben von Prof. Dr. J. W. SPENGEL in Giessen.
Dreizehnter Band, 3. Heft. 1900.
Verlag von GUSTAV FISCHER in Jena.

Table of Contents.

I. Introductory.
  1. Review of Literature.
    a) The Mesomeres of the Cephalic Region.
    b) Segments of the Encephalon.
  2. Manipulation of Material.
    a) Living Embryos.
    b) Dissected Specimens.
    c) Sections.
II. Descriptive.
  A. Encephalic Segments of Teleosts.
    a) Neural Segments of Salmo observed in Living and Dissected Embryos.
    b) Neural Segments of Salmo observed in Divided Embryos.
  B. Encephalic Segments of the Chick.
    a) Embryos with open Neural Grooves, 1—6 Somites, Ages 21—25 hours.
    b) Embryos with 6—7 Somites, Ages 25—26 hours.
    c) Embryos with 7—20 Somites, Ages 27—40 hours.
    d) Embryos 40—100 hours old.
  C. Study of Sections. Chick and Trout.
    a) Segmental Criteria.
    a) Histology.
    c) Nerve Relation.
III. General Considerations.
    Identification of Neural Segments.
    Neural Segments in Teleosts, Historical and Critical.
    Neural Segments in the Chick, Historical and Critical.
    Value of various segmental Criteria.
    a) Mesomeres.
    b) Branchiomeres.
    c) Neural Segments.
    Summary.
  Bibliography.
  Plates.

Developmental History of Primary Segments of the Vertebrate Head [1].

I. Introductory.

1. Review of Literature.

That the Vertebrate head is composed of segments similar to those that constitute the trunk, has gradually become a fixed point in philosophical morphology. Although there is no dissent upon the question of the segmental nature of the Vertebrate head, the question of what constitutes the criteria of the segments, of what is their number and their anterior limit, is still under controversy. There has been a gradual change of front and the evidence has been shifted from sutural joints (Oken, 1807; Goethe, 1820; Owen, 1832), to cranial nerves (Huxley, 1859), to branchial clefts and cranial nerves (Gegenbaur, 1878), head cavities (Balfour, 1878; Van Wijhe, 1882, and others), and finally to segments of the neural tube (Béraneck, 1884; Orr, 1887; McClure, 1860; Waters, 1892; Locy, 1895).

The literature in all these lines has been reviewed somewhat extensively and it seems necessary for the purpose of this paper to give only a brief review of the more important results attained by study of a) the Mesoderm of the Cephalic Region, and b) the Segments of the Encephalon.

a) The Mesomeres of the Cephalic Region.

Balfour pointed out in 1878 that the mesoblastic somites are present in the head in a modified form. To them he gave the name of head cavities and suggested that they are homologous with the mesoblastic somites of the trunk. The subject was further advanced by Marshall, '78 and '81, and by Van Wijhe, '82, whose paper has been accepted as the standard reference for cephalic segments in the Elasmobranchs. He described nine cephalic mesomeres in *Scyllium* and *Pristiurus*. These observations inaugurated a new era in the investigation of the problem of head segmentation, based upon the study of Selachian embryos.

The post-otic segments of Van Wijhe have been verified by many observers who agree further that these segments are serially homologous with the myotomes of the trunk. The pre-otic region,

---

[1] Contribution from the Zoological Laboratory of Northwestern University under the direction of Wm. A. Locy.

however, constitutes a disputed territory. RABL, '92, finds but three segments in this region, while DOHRN, '90, has observed from twelve to fifteen. The following brief review will show that there is also lack of harmony regarding the morphological value of these segments.

AHLBORN, '84, verifies the work of VAN WIJHE with one exception — he makes one mesomere out of VAN WIJHE's segments 3 and 4. He reaches the important conclusion that branchiomeres are independent of mesomeres, and that the cephalic mesoderm presents a typical metamerism "which developmentally is in perfect harmony with the primary trunk somites".

GEGENBAUR, '87, considers VAN WIJHE's head somites very dissimilar structures. The 7th, 8th and 9th, he classifies as cænogenetic, those cephalad to these he designates as palingenetic. He believes there was originally complete concordance between branchiomerism and mesomerism, but that subsequently, by a disappearance of some branchial arches, trunk segments are projected forward. He discredits the segmental value of VAN WIJHE's first mesomere and is of the opinion that the present number of cephalic segments gives no trustworthy indication of the ancestral history.

According to KASTSCHENKO, '88, the anterior trunk somite in Selachian embryos is the first ontogenetic mesomere. To this, new segments are added both caudad and cephalad, the latter growing more and more indistinct towards the cephalic end where they finally disappear in the vicinity of the first gill clefts. Between the first and third gill clefts the evidence of metamerism is so indistinct that the author is unable to determine the number of segments in this region. He confirms the observation of AHLBORN regarding the independence of branchiomeres. He is also inclined to discredit the morphological value of these "head cavities" as segmental organs and says (in: Anat. Anz., V. 3, p. 761): "Although I do not agree with VAN WIJHE as to the morphological interpretation of the head cavities, yet their ultimate fate, as described by this author, I completely confirm" (Author's translation).

The following year RABL, '89, expresses the view that the 5th to 9th somites of VAN WIJHE represent true metameres but believes the segments cephalad to these are structures *sui generis* to which must be assigned a different morphological value. In '92 the same opinion is again expressed.

In the pre-otic region of *Torpedo marmorata*, 3 mm long, DOHRN, '90, finds 13 to 15 segments, which, taken with the four post-otic segments, that he considers homologous with Van Wijhe's 6—9 somites, makes a total of 18 to 19 cephalic mesomeres. Killian, '91, confirms this with one correction finding 17 to 18 segments. Miss Platt, '91, adds an anterior cavity in *Acanthias vulgaris* to Van Wijhe's nine mesomeres. She also finds one cephalic segment caudad and reports one between Van Wijhe's 3rd and 4th segments making a total of 12 cephalic mesomeres. Hoffmann, '94, reports ten in *Acanthias* adding one caudad to the 9th observed by Van Wijhe.

Van Wijhe, Dohrn, Killian, Miss Platt and Hoffmann, regard these cephalic segments as serially homologous with the somites of the trunk proper.

Sedgwick, '92, records a variable number of cephalic mesomeres and doubts their segmental value. In support of this view he offers the following argument (in: Quart. Journ. micr. Sc., V. 33, p. 576): "But even if Dohrn is right in his enumeration of the anterior somites, it is clear that *Torpedo* differs from *Scyllium*, *Raja* and *Pristiurus*, whether my account or Van Wijhe's be taken as correct. For in *Torpedo* there are four somites where in the other genera there is most unquestionably one, e. g. the somite of Wijhe. It would appear, then, that if the number of primitive cranial somites in any given region of the head does really differ in closely allied genera in the manner indicated by the divergent observations of Van Wijhe, Dohrn, Killian and myself, the supposed indications of segmentation which are found in the adult and are constant throughout the Vertebrata can have very little value as real tests of primitive metameric segmentation. We may, I think, even go further and say that the adult arrangement of nerves and branchial arches, etc., characteristic of the Vertebrate head, must have arisen subsequently to the disappearance of primitive segmentation."

Kupffer, '92, who has given much study to the head cavities in *Acipenser* and *Ammocœtes* writes as follows (in: Ergebn. Anat. Entw., V. 2, p. 522): "I assume that these head-cavities represent rudimentary gill pockets which upon the disappearance of the old mouth of *Palæostoma*, lost their function. On the contrary their origin as direct diverticles of the fore-gut clearly indicates that they are visceral clefts."

It is a significant fact that Hatschek, '92 (according to Kupffer, '92), has found seven pair of entodermic evaginations in the cephalic region of *Amphioxus*, which in later stages become constricted from the foregut and occupy a position ventrad to the segmented mesoderm. As to the ontogenesis of these pockets that Hatschek regards as rudimentary, he says (in: Verh. anat. Ges., 1892, p. 144): "Symmetrical in their origin they become in later development unsymmetrical, the right one is extended and the epithelial cells of the wall become quite flat and enclose a large triangular space, ventral to the chorda, in the anterior end of the body. The left sac has a thick wall, develops cilia and takes a diagonal position under the chorda, and finally forms a little opening on the left side after dividing into two divisions. The division on the left side which has the external opening is wider and ciliated, the one to the right forms a blind pocket and is narrower. The external opening which enlarges is ventral and to the left of the chorda" (Author's translation).

Sewertzoff[1]), '95, is unable to find pro-otic segments in embryos of *Acipenser* and *Siredon*. After a careful review of the literature he concludes that "between the auditory vesicle and the anterior dorsal arch of the occipital region three somites are found in the shark (the 5th, 6th and 7th somite); but only two in Amphibia and Birds. In Amphibians (Anura) and Birds, one more mesodermic segment is found in the pro-otic region. In this manner the conclusion to which we come is as follows: there was a time when the cephalon was segmented in the ancestors of the present vertebrates. . . . The somites that lie in front of the 2nd somite of the meta-otic region of the Urodeles [which corresponds to the 7th head somite of the shark (Van Wijhe, Hoffmann) and the 6th of the lamprey (Hatschek)], are segments common to all Craniota and consequently primitive head metameres. Gradually the following segments which originally belonged to the trunk were added to the component elements of the head; at first the occipital arch and the myotome which lies before it, the Urodeles have remained at this stage which is common to all Gnathostomata; in Anura another myotome is added to the head; finally we have in the case of Fishes, Sauropsida and Mammalia the most complete expression of this process, a whole series of trunk segments being added to the component elements of the head. In general the evolution in the back part of the head can be traced to the disappearance of metameres which took place from in front backwards and to the gradual transformation of the front segments of the trunk into the back part of the head" (Author's translation).

In 1898 the same author reports 9 cephalic segments in *Pristiurus* and 10 in *Acanthias*. He thus confirms the observations of

---

1) in: Bull. Soc. imp. Nat. Moscou, No. 2, p. 273.

Van Wijhe and **Hoffmann**. In *Torpedo*, however, he finds 13 mesodermic segments. According to **Sewertzoff** one segment in *Acanthias* and four in *Torpedo* have been added to the cephalic region, caudad at the expense of the trunk proper. In this short communication the author refrains from a discussion as to the morphological value of the pre-otic segments.

The review of literature, with exception of the last author quoted, has dealt largely with cephalic metamerism of Selachians. In other Vertebrates, the mesodermic head cavities appear indistinct, and but few observations are recorded upon them. **Scott** and **Osborn**, '79, were probably the first to observe series of cœlomic cavities in the head of Amphibian embryos. Miss **Platt**, '94, finds in *Necturus* 4 pre-otic and 5 meta-otic segments which she considers homologous with the nine conventional segments described by **Van Wijhe**. **Houssay**, '90, has observed 11 in the Axolotl, while **Oppel**, '90, in *Anguis* embryos describes **Van Wijhe**'s 1st to 3rd and 6th to 9th segments. Lastly, **Goronowitsch**, '92, finds one pre-otic and two post-otic segments in embryos of the chick. They are very transient and are present in embryos with 6 to 9 somites.

The review of literature dealing with the cephalic mesomeres makes two points clear:

1) Observers disagree as to the number of pre-otic segments.
2) They disagree as to their morphological value.

The discrepancies in observation and disagreement in interpretation of head cavities is more extensive than is usually recognized. The natural presumption is in favor of making the mesomeres of the head carry the marks of primitive segmentation — as they do in the trunk, but it is worth while to keep in mind **Sedgwick**'s suggestion that evidences of primitive segmentation will appear early in developmental history and that the metameric arrangement of head cavities as well as nerves and branchial arches may have arisen "subsequently to the disappearance of primitive segmentation".

b) Segments of the Encephalon.

A revival of interest in the problem of head segmentation came with the relatively recent discovery that the entire neural tube of young Vertebrate embryos is divided by transverse constrictions into similar segments. The case presented by those segments has been especially strengthened by showing (**Locy**, '93) that they antedate the mesomeres even of the trunk region. On the whole there is better agreement among the observers as to the number and character of these segments than there is as to the mesoblastic divisions of the head. The chief differences lie in reference to the fore- and mid-brain regions.

Early observations of folds in the hind-brain are recorded by **von Baer**, '28, who saw them in the chick during the third day of incubation; by **Bischoff** who found them in the dog; by **Remak**, '50, who suggested a possible nerve relation, and by **Dursy**, '69, who counted six folds in the hind-brain of the embryonic cow. **Dohrn**, '75, contrasted this segmentation in the medulla of bony fishes with the metamerism of insects, thus suggesting a segmental value. **Mihalkovics**, '77, and **Balfour**, '81, were inclined, however, to give a mechanical interpretation to them.

Although **Remak** in 1850 had suggested that the segments of the medulla possibly bore a definite relation to the cranial nerves of that region, this relationship was not determined or placed on a substantial basis till **Béraneck** in 1884 showed that, in embryos of *Lacerta agilis*, from 3 to 7 mm in length, the connection of cranial nerves with definite segments of the medulla was both constant and regular. **Béraneck** thus contributed the first real factor in establishing their segmental relations. In 1887 he reached similar conclusions from observations on embryos of the chick.

Kupffer's observations are extensive and cover a period of several years. In 1884 he describes five segments in the medulla and three in the mid-brain of trout embryos, 18 to 20 days old, assigning to them a segmental value. He also finds five segments in the medulla of Mammalia. In the following year '85, he observed in young embryos of *Salamandra atra* with a wide open neural groove eight cephalic segments. Each segment is bounded anteriorly and posteriorly by transverse folds that occupy the median part of the cephalic plate but does not effect the margins of the neural groove. In 1893 in his "Vergleichende Entwicklungsgeschichte des Kopfes der Cranioten" he reprints these conclusions.

Orr, '87, describes in detail six segments in the hind-brain of *Anolis* and traces very definitely their connection with the cranial nerves of this region. He discusses the histological condition of these segments ("neuromeres") and gives five criteria by which a typical segment may be identified. (A discussion of these criteria appears below.) He finds no neuromeres in the encephalon cephalad to the mid-brain but assumes that in ancestral forms there was a segmental condition of this region.

Hoffmann, '88, reports seven segments present in the hind-brain of *Lacerta* and *Tropidonotus*, adding one cephalic segment caudad to the six neuromeres that **Orr** described in *Anolis*. The author differs somewhat from **Orr** as regards the relationship of the cranial nerves to these segments.

Miss **Platt**, '89, divides the encephalon of the embryonic chick into seven primary segments. Five of these are in the medulla, the cerebellum constitutes one and the primary fore-brain and mid-brain one. From her descriptions, it appears that the "neuromeric segmentation" has been confused with the division of the front end of the neural tube into brain vesicles.

McClure, '90, demonstrates neuromeric segmentation throughout the neural tube and also verifies, in the chick and lizard, **Orr**'s hind-brain neuromeres but finds only five segments in this region in *Amblystoma.* He finds two neuromeres in the fore-brain and assumes, from the examination of figures, the existence of two in the mid-brain.

Waters, '92, decides that there are three neuromeres in the fore-brain of Teleosts; two in the mid-brain and six in the hind-brain, making a total of eleven in the entire encephalon. He confirms the observation of **McClure** regarding the presence of but five neuromeres in the hind-brain of *Amblystoma* but suggests that the reduction is probably due to a fusion of two segments.

Froriep, whose contributions like those of **Kupffer** extend over a number of years, finds in embryos with the neural groove widely open, five segments in the cephalic plate of *Triton cristatus* and four in *Salamandra maculosa.* In 1891, he finds two segments in the diencephalon and three in the mesencephalon of the mole and assigns to them a metameric value. The next year he withdraws from this position and says: "the segmentation is merely passive mechanical results of rapid longitudinal growth in a limited space and has therefore no morphological significance." The early neural segments detected by **Kupffer** in *Salamandra atra* he believes to be the result of underlying mesoderm-somites and concludes that "The jointing of the Vertebrate body is dependent upon the middle germ layer".

Herrick, '92, finds six neuromeres in the medulla of Ophidian embryos and makes the very pertinent statement: "if neuromeres once existed in the fore-brain they would only be visible at an early stage and would be obscured by altered conditions".

According to **Zimmermann**, '91, there are eight encephalomeres in Salamander embryos in front of the first protovertebra. The three cephalad encephalomeres are large and subsequently divide, the first into two and the second and third each into three, making a total of 13 cephalic segments. The author thinks the three large cephalad encephalomeres are originally compound and that for some reason the subdivision is retarded in this region.

Finally, **Locy**, '95, traced the segments of the neural tube in sharks back to very early embryonic stages before the eyes evaginate or the somites of the body appear and claimed that they are identical with the neuromeres of **Orr** and **McClure**. The results of my studies on chick embryos tend to confirm the very early appearance of the neural segments and to show that they are identical with the neuromeres so widely observed in later stages. **Locy** finds eleven segments in front of the origin of the vagus nerve, six in the hind-brain, two in the mid-brain and three in the primary fore-brain. Later in the ontogeny three segments from the spinal cord are incorporated in the cephalic region, making a total of 14 cephalic segments. **Neal**, '98, working upon the same material, finds the segments described by **Locy** in the early embryonic stages but claims for them great irregularity, and, failing to find them in embryos with closing neural groove concludes that the early segments are mechanical formations and in no way related to the neural segments that are present later in the ontogeny. With **Van Wijhe** he finds nine cephalic mesomeres and also describes seven encephalomeres, distributed as follows: the fore-brain one, the mid-brain one, and the hind-brain five.

Two important conclusions in reference to neuromeres appear from the above review:

1) There is substantial agreement among observers as to the six segments in the hind-brain, their nerve relation and metameric value. When more than six have been observed (**Hoffmann**, '90, **Locy**, '95) segments caudad to the true sixth have been counted.

2) There are but few observations on the encephalic segments that lie in front of the cerebellum.

The following observations on the primitive segments of Teleost and chick embryos were made during 1898 and 1899 in the Zoological Laboratory of Northwestern University. It is a pleasure to acknowledge here my great indebtedness to Dr. Locy, the Director, for constant suggestions and for his interest and assistance during the whole period of my work. The observations show the very early appearance of neural segments and their identity with the neuromeres of Béraneck, Orr McClure and others. They show clearly in the earliest stages the condition of the primary segments of fore- and mid-brains, and stages in their modification up to the time the segments become obliterated by the expansion of the brain wall of this region.

The experience gained by the author in tracing the history of the epiphysial vesicles in Teleosts (Hill, '91 and '94) afforded a valuable and really essential preliminary training for the work involved in this paper¹).

2. Manipulation of Material.

As the work contemplated the study of these segments first in the living embryos, chick and Teleosts were selected. It should be remembered such a study presents many difficulties. The study of a single living embryo is necessarily limited in time. The material cannot be laid aside and the observation repeated at a later date. Neither as a rule is a comparative study of different ages possible. The transparent nature of the embryos often leads to confusion because segments of the two sides may appear indiscriminately mixed. This is especially true of side views when studied under the compound microscope. A good dissecting microscope gives in many ways better service, as it enables the operator to manipulate his material to greater advantage. This is especially true of preserved embryos when studied as opaque objects where delicate shadows serve to detect segments.

The following Teleosts²) were studied: *Salmo fontinalis* (Mitch.), *S. purpuratus* (Pallas), *S. fario* (L.) and *Coregonus albus* (Ger.). In order to repeat observations upon living material, cultures were reared differing in age from 6 to 10 days. The temperature of the lake water where these developed was 10 degrees colder than the

---

1) As early as 1890, observations were begun by the author, on neural segments of Teleosts, in the University of Michigan, at the suggestion of Prof. Reighard, but were discontinued in order to follow the history of the epiphysial outgrowths in the same group of animals.

2) I desire to express my thanks to the United States Board of Fish Commissioners for liberal supplies of Teleost material.

water of rivers where the eggs at hatcheries are reared. Growth therefore was retarded so that embryos 25 days old were approximately developed no farther than those 20 days old at the hatcheries. An allowance of 4 to 7 days must be made if the age of the embryos described is compared with the age of embryos that develop in hatcheries at the normal or higher temperature.

The gelatinous envelope of the *Salmo* egg was removed before the embryo was killed with the fixing reagent. The living embryos sketched were numbered and the observation repeated upon the preserved specimen. In dissecting preserved material it was soon discovered that the most desirable specimens to begin work upon were embryos with 35 to 40 somites where the neural segments of the medulla are very prominent. These segments were then traced through a close series of younger stages as well as in older forms. Furthermore, as the segments appear as a rule more distinctly on the inner aspect of the brain wall, it became desirable to expose this surface. This can be done by dissecting away one side of the brain wall or dividing the embryo into lateral halves. The latter form of manipulation gave very satisfactory results in *Salmo* material but with chick embryos this process was less satisfactory on account of the hollow nature of the neural canal.

Finally the embryos were sectioned in the ordinary way and the sections studied in the light of the knowledge gained from the study of the living and dissected specimens. Without this knowledge the study of sections would certainly lead to confusion if not error. The secondary divisions that frequently are present would eventually be confused with the primary ones.

The conventional way of studying cephalic metamerism has been almost exclusively by the process of sections. Locy, '95, diverged from this method by dissecting away the cephalic mesoderm in embryos of the shark, and thus exposed the entire encephalon with its segmental folds. I have used this method with gratifying results in embryos of both the chick and the trout. By sweeping the neural tube clean from all surrounding tissues, it is certainly true that with properly reflected light, neural folds can be detected in this manner that could not be observed in any other way.

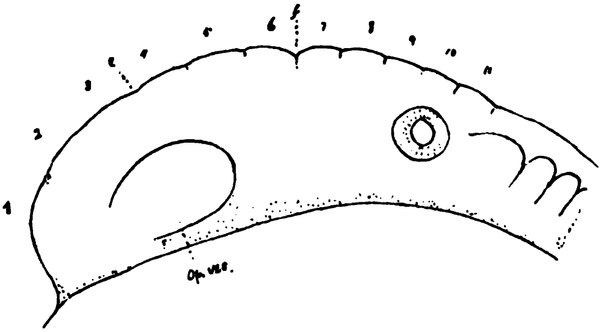
II. Descriptive.

A. Encephalic Segments of Teleosts.

a) Neural Segments of *Salmo* observed in Living and Dissected Embryos.

I have found 11 encephalic segments in *Salmo*, and have traced their history from embryos with 19 somites, 16 days old, up to embryos with 35 somites, 38 days old.

Fig. A.



Sketch A is a camera tracing of the anterior portion of a living embryo of *Salmo purpuratus*, 16[1]) days old. The optic vesicles are present as two solid, elliptical, cellular masses that are turned caudad and applied closely against the lateral walls of the encephalon (*op. ves*). The proliferation of the optic vesicles begins in embryos two days younger. Sections of embryos of this age reveal the presence of the lens, which is still attached to the epiblast. The central canal of the neural axis has not yet appeared. Along the dorsal crest of the cephalic region are 11 transverse grooves or constrictions that divide the encephalon into 11 segments or joints (*1—11*). The transverse groove (*f*), that lies midway between the optic and the auditory vesicles, is deeper than the other grooves and marks the posterior border of segment 6, which later forms the cerebellum. It is desirable to call particular attention to this groove, as in later stages it becomes very conspicuous and forms clearly the dividing line between the cerebellum and the medulla, enabling us thus to identify with

---

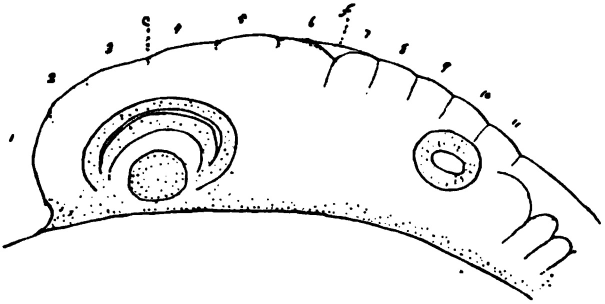
1) See observations on age in relation to temperature of the water p. 13.

certainty the anterior limit of the latter. Caudad to this depression there are five distinct segments that constitute the medulla (*7—11*).

The auditory vesicle lies opposite segment 10. Caudad to this vesicle and at a distance equal to two segments of the medulla, or approximately to the width of three myalomeres, is the first body somite. I was unable to observe, at this stage, any segmentation in the heavy mesoblastic pad that occupies the space between this somite and the auditory vesicle.

Cephalad to the deep groove (*f*), the neural axis is divided into 6 segments by the presence of five transverse dorsal grooves, that appear fainter but otherwise resemble the grooves that divide the medulla into segments. The one between segments 3 and 4 (*c*) is deeper than the other four, and as the posterior commissure later appears at this point, we may speak of this groove as the dividing line between the primary fore-brain and mid-brain. The former is therefore made up of three segments (*1—3*); the mid-brain and cerebellum likewise of three segments (*4—6*). As will appear later, segment 6 develops into the cerebellum and segments 4 and 5 therefore represent the mid-brain. In older embryonic stages these encephalic divisions become very distinct and can be traced with accuracy in both living and dissected as well as divided specimens.

Fig. B.



In a living embryo, two days older (sketch B), the head fold is a little deeper, and the optic vesicle, which now presents a cavity, is folded back upon itself to form the optic cup. The lens is completely constructed from the epiblast. The auditory vesicle lies a little farther caudad and partly covers segments 10 and 11. The 11 encephalic segments are present as described in sketch A, but the dividing grooves are deeper and can be traced a short distance down the sides of the neural axis. The first indication of a true neural canal has appeared as a fine median cleft dividing the neural axis into lateral halves. Again the dorsal groove (*f*), that marks the posterior border of the cerebellum, is deeper than any of the other encephalic constrictions. A lateral neural expansion has taken place in this vicinity, which with the formation of the neural canal, leaves a thin transparent roof covering this depression.

The six segments in front of the constriction (*f*) have become more distinct. The dorsal depression (*c*), which separates the primary fore-brain from the mid-brain, can be identified by its position which, as in sketch A is dorsal to the middle of the lateral eyes, and also by the fact that it is deeper than the other segmental constrictions of this region. The segments otherwise are both uniform and constant and resemble those of the medulla, except in degree of distinctness.

Thus far these segmental grooves have been described as though they were confined exclusively to the dorsal region of the encephalon. In living embryos, 16, 17 and 18 days old, I have been able to observe them only in this region. In older embryos, however, both in living and dissected specimens, these grooves can be traced ventrally around the encephalon. The many difficulties involved in dissecting them in the early stages render it possible that in embryos 16—18 days old they encircle the encephalon just as they do in older forms, but partly on account of their delicacy because the cephalic mesoderm is more dense towards the ventral region of the encephalon, I have only been able to observe them along the dorsal zone. For like reasons I deem it very probable that these segments are present in even younger embryos than 16 days old.

In hardened embryos, 19 days and older, the brain walls have been laid bare by complete removal of the cephalic mesoderm and the brain thus exposed has been studied by reflected light. Fig. 1, Plate 28, represents the right profile view of the encephalon of an embryo 19 days old, with 29 somites, prepared in this manner. The thin transparent roof of the medulla is removed. Fig. 2 is a dorsal view of the same specimen. In this case it is clear that the transverse grooves pass externally down the lateral walls and ventrally around the whole neural axis.

Having removed the large lateral eyes and the cephalic mesoderm, the five anterior grooves are much better observed than is possible by the study of the living embryo. The auditory vesicle in this specimen lies nearly opposite segment 10, its posterior margin overlapping a part of segment 11. The lateral expansion that was mentioned in describing 18 day embryos (sketch B) has gradually increased and involves the dorsal portion of segments 6 and 7. It should be remembered that only the anterior half of this expansion, or segment 6, represents the cerebellum. In profile view, Fig. 1, it will be seen that ventrally, this expansion is slightly directed cephalad.

The transverse constrictions that mark the limits of the five cephalad segments are less distinct than those of the medulla, but like the latter pass ventrally around the encephalon (Fig. 1). Segment 1 is elliptical and forms the front end of the neural axis. Segment 2 has the form of a wedge. Its broad end is turned ventrad and slightly expanded to form the first traces of the infundibulum (*inf*). Segment 3 has also the form of a wedge but in this case the broad end is turned dorsad. These three segments (*1*, *2* and *3*) develop into the primary fore-brain as will appear more clearly in later stages. The two segments of the mid-brain (*4* and *5*) are also well defined by the presence of external, transverse, segmental grooves.

The presence of these transverse grooves in the fore-part of the brain gives a clear picture of segments or joints. As these grooves at this stage of development encircle the neural axis the segments embrace both dorsal and ventral zones. As will be observed later the appearance of the inner walls of the fore- and mid-brains in the specimens is worthy of especial notice. The lines separating the segments are definite and the number of segments can be counted on both the inner and the outer aspect of the encephalon. In both cases, there are 5 segments in this region, 3 in the primary fore-brain and 2 in the mid-brain. The transformation of these segments is interesting and if closely followed clears up some obscure points: 1) The most anterior segment is that of the olfactory, or segment 1. 2) The optic nerve and the infundibulum come from segment 2; the pineal outgrowth from the roof of segment 3.

Fig. 3, Plate 28, shows the left profile view of the encephalon of a dissected embryo 22 days old, with 34 somites. The lateral expansion of segments 6 and 7 is no longer restricted to the dorsal region but affects the ventral portion of these segments. The ventral growth of the second segment to form the infundibulum is much advanced and has its distal end directed caudad. In the ventral and anterior margin of this segment is a small circular depression (*opt. n*) which marks the union of the optic stalk with the encephalon.

Fig. C.

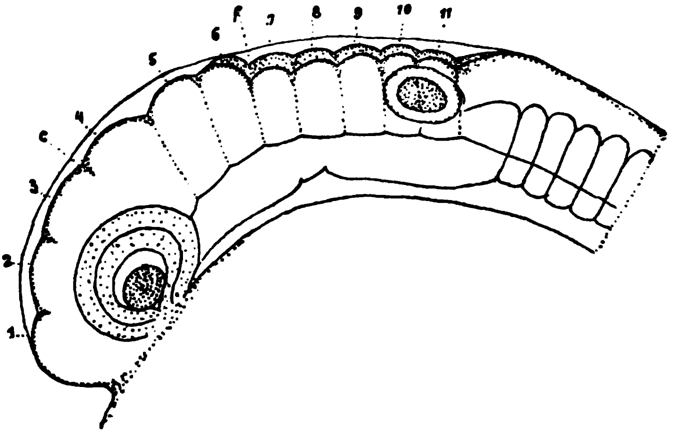


Fig. 4 and sketch C are camera drawings of a living embryo of the same age as the one just described. A thin transparent unsegmented roof covering the encephalic segments, has been formed. The segments of the medulla are very distinct, the segmental grooves passing directly across the floor of the 4th ventricle to be continued, in the same transverse plane, on the external surface both laterally and ventrally.

As was observed in younger embryos, the dorsal groove (*f*) which marks the anterior limit of the medulla, continues to be deeper than any of the other dorsal constrictions. The first two grooves cephalad to this, mark respectively the anterior limit of the cerebellum and the second segment of the mid-brain, and can be traced around the encephalon in a manner similar to the grooves of the medulla. The three grooves anterior to these are less distinct. The posterior limits of segments 1, 2 and 3, could be detected only along the dorsal encephalic crest. In view of the fact that these grooves are very distinct on both the inner and the outer surfaces of the encephalon, in divided and dissected embryos of this age as will be shown later, I have concluded my failure to trace them ventrally along the sides of the brain in living embryos, was due to the presence of the eyes that are closely applied to the brain wall of this region, and also to the cephalic mesoderm that forms a dense tissue just dorsal to the optic vesicles.

Figs. 5 and 6 present dorsal and lateral views respectively of the cephalic portion of a living embryo 23 days old, with 25 somites.

In the dorsal view (Fig. 5) it will be observed that a lateral expansion has taken place both caudad and cephalad to the deep constriction (*f*). The expansion involves segments 6 and 7 and occurs also in the chick. The limits of the five anterior segments were marked by both external and internal transverse grooves and these segments could therefore be clearly counted.

Since segments 2 and 3 are reciprocally wedge-shaped their relative width in a dorsal view depends upon the optic plane in which they are observed. The camera tracing of Fig. 5 is taken from a median horizontal plane, and segments 2 and 3 are therefore equal in size.

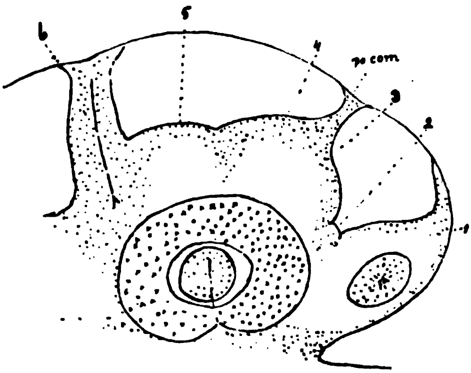
As can be seen in the profile views, the embryos at this age are curved ventrally to conform to the spherical yolk upon which they rest. Fig. 5 was sketched from two points of view. A camera tracing was first made of that portion of the head in front of the cerebellum. The embryo was then rotated, till the line of vision formed a right angle with the horizontal plane of the medulla and another sketch made and attached to the former. Fig. 5 thus represents the cephalic end, not curved, but straightened.

Fig. 5 should be compared with Fig. 7, which shows the dorsal view of a living embryo, 26 days old, as seen from one point of view only. In the latter, the medulla is very much fore-shortened, and the mid-brain much expanded laterally and presenting distinctly two segments (*4* and *5*). The primary fore-brain appears as a narrow tube closely compressed between the large lateral eyes. The region including the primary fore-brain and mid-brain, thus have become pear-shaped with the pointed end turned cephalad. The three segments of the fore-brain show in this view. The second (segment 2) is very narrow in the dorsal region and widens ventrally (see side views), while segment 3 is relatively broad in the dorsal region but very narrow in the ventral zone.

In dissected embryos one day older (Fig. 8) than the one just described, the expansion of the cerebellum (segment 6) is very distinct. The transverse external groove that marks its anterior limit, and thus separates the cerebellum from the mid-brain, has become deep and passes from the dorsal crest of the encephalon laterally and ventrally towards the base of the brain where it disappears. The dorsal groove (*f*) that forms its posterior limit, still continues to be deeper than the other transverse grooves of the medulla. The segments of the latter have passed ventrad, a process that appeares to accompany the encephalic expansion that was mentioned in the description of Fig. 5.

From an external view five segments can still be detected in that portion of the brain that lies cephalad to the cerebellum (*1—5* Fig. 8). The anterior segment in profile view appears somewhat elliptical. Segment 2 has become very narrow dorsally while ventrally it expands into the relatively large infundibulum, which is directed caudad and extends back to a point opposite the middle portion of the mid-brain. Segment 3 is dorsally very broad while ventrally it tapers to a point. Externally the mid-brain now appears unsegmented, save for a ventral constriction that lies just dorsal to the posterior margin of the infundibulum.

Fig. D.



Sketch D is a camera tracing of the cephalic end of a living embryo, 32 days old, rotated towards the right and viewed from a point slightly in front and above the embryo. The sketch was made to show the position of the posterior commissure (*po. com*) which at this age is present as an opaque transverse band of fibres that pass across the roof of the encephalon and unite on each side with the anterior portion of segment 4 and the posterior portion of segment 3. Simultaneously with the formation of the commissure, a groove or notch appears in the same position in the dorsal wall of the brain. This groove has thus a different history from those that are present in the base of the brain and therefore a correspondingly different morphological value.

The oldest living embryo in which I have been able to satisfactorily observe the presence of neural segments is represented by Fig. 9. The segments of the medulla are fainter than in earlier stages but it should be noted that they can be traced in the fore- and mid-brain regions as well as in the medulla. In front of the cerebellum the two segments of the mid-brain (*4* and *5*) can be seen on the inner aspect of the encephalon through the transparent brain wall. In like manner the three segments of the primary fore-brain appear (*1—3*).

These five segments of the anterior cephalic region are now confined to the floor and sides of the brain in a manner very similar to the five segments of the medulla. In both regions the segments at this age are covered by an unsegmented, thin and very transparent roof.

Closely applied against the lateral wall of segment 1 is the olfactory pit (*olf.pt*). As in other specimens, the dorsal portion of segment 2 is very narrow. The transverse dorsal depression formed by the fibres of the posterior commissure (*po. com*) has become deeper than in earlier stages (sketch D). Just cephalad to this depression near the median plane, are the two evaginations that form the right and left epiphysial vesicles whose history I have traced in former contributions (Hill, '91 and '94).

b) Neural Segments of *Salmo* observed in Divided Embryos.

The neural segments previously described are even more favorably seen by observing embryos that have been divided into lateral halves. The inner surfaces of the brain-walls are thus exposed entirely free from any cell layers. This form of manipulation can be used only after the neural cavity is fully formed (embryos about 20 days old, 31 somites). Between 20 and 36 day — stages I have a very complete series of divided embryos and have been able to trace in them unbroken continuity of the segments, but I shall limit the description to a few typical stages.

Fig. 10 represents the inner surface of the right cephalic half of a divided embryo 20 days old with 31 somites. Eleven transverse grooves are present that divide this surface into 11 segments (*1—11*). Fig. 10 compared with Fig. 1, representing the external encephalic surface of a dissected embryo one day younger, shows that the external grooves of the latter correspond with internal grooves of the former and thus divide the neural axis into comparable segments.

As represented in this figure (Fig. 10) the first five segments, that form the primary fore-brain and hind-brain, are more distinct when viewed in the divided embryo than when studied in the dissected or the living specimens. In this view the anterior segment is biconvex, the greater curvature forming the front of the neural axis. Segment 2 is dorsally narrow while ventrally it is broad and slightly expanded in a caudad direction to form the first traces of the infundibulum (*inf*). Towards the ventral portion of this segment there is present a small pit or depression (*op.n*). This is the remnant of the lumen that primarily communicated with the holow optic stalk. Segment 3 is dorsally broad and tapers ventrally. Its posterior limit in the dorsal region is marked by a depression (*c*) which in older stages marks the position of the posterior commissure and therefore forms the posterior limit of the primary fore-brain. Between this depression (*c*) and the deep constriction (*f*) which, as previously observed, forms the anterior limit of the medulla, three segments are present (*4*, *5* and *6*). One of these, segment 6, is the cerebellum and the other two, segments 4 and 5, represent the mid-brain. The transverse grooves that divide the anterior encephalic region into segments are distinct and can be counted with as much accuracy as the transverse grooves that divide the medulla into corresponding sections or joints. In both regions the segmental grooves are better defined on the internal than the external brain surface.

In divided embryos two days older, a very considerable change has taken place on the inner aspect of the encephalon. This change is represented in Fig. 11 which should be comparad with Fig. 3. The latter represents the external surface of the same age. In the divided specimen (Fig. 11) the deep constriction (*f*), that forms the anterior limit of the medulla, is at once very apparent. The region in front of this constriction constitutes, therefore, the primary fore-brain, mid-brain and cerebellum and it is a great satisfaction to have the segmental joints so distinctly marked in the controverted territory of fore- and mid-brain. Segment 1 is elliptical and is but little changed, either in form or position from the description given of it in Fig. 10. Segment 2, not only tapers dorsally but has expanded ventrally in a caudad direction to form the relatively prominent infundibulum (*inf*). Segment 3 tapers ventrally and, as in Fig. 10, has at its posterior dorsal margin a depression (*c*) which, as stated before, marks the posterior limit of the primary fore-brain. A horizontal furrow intercepts the two segments of the mid-brain giving them thus a dorso-ventral length equal approximately to the length of the segments of the medulla, and like the latter, have become covered by an unsegmented brain-roof. The developmental history of this horizontal furrow clearly shows that it has no segmental value. Because of its prominence in older embryos it seems desirable in this place to trace this history.

In divided embryos 24 days old (Fig. 12) the horizontal furrow, mentioned above, is deeper and longer, and forms not only the dorsal limit of the two mid-brain segments but extends over the cerebellum and in front, above the third segment of the fore-brain. From my observations on living embryos and from a study of sections, it appears that this furrow is produced by a reduction of cellular elements on the inner surface of the brain wall of this region. This reduction spreads dorsally so as to form two diagonal furrows (Fig. 12). In later stages the inner wall of the brain-roof of this region presents a ragged appearance (Fig. 13), while in still older embryos the surface becomes more even (Fig. 14) and ultimately smooth (Fig. 15). During this process the outer surface is unaffected while the brain-roof becomes very thin. The method of their appearance and their history indicate that these furrows are not of segmental value.

If we now return to the segmental condition of embryos 24 days old (Fig. 12) as observed in divided embryos, we find in this stage, the five anterior segments (*1*—*5*) confined to the base and the lateral walls of the encephalon. In this respect they resemble the segments of the medulla (*7*—*11*). The three segments of the primary fore-brain are present as described in Fig. 11. The groove that separates segment 3 and 4 and forms the posterior limit of the primary fore-brain has become very indistinct. On the other hand the constriction that separates the two segments of the mid-brain (*4* and *5*) is deep. The five anterior encephalic segments can thus be counted and are similar both in position and form to the five segments (*7*—*11*) of the medulla.

Fig. 13 shows the inner surface of the encephalon of a divided embryo 26 days old. Segment 2 is more compressed in the dorsal region than in younger embryos, while its ventral expansion, that forms the infundibulum, is much enlarged. In the dorsal region segment 3 is broad and presents a depression which at this age gives the segment when sectioned, the appearance of being double (Fig. 43). The two segments of the mid-brain (*4* and 5) and segment 6, the cerebellum, are very distinct. The latter alone extends to the dorsal surface of the brain. The depression (*f*) remains conspicuous as observed in other specimens. From the bottom of this depression several secondary grooves radiate into the base of the brain. From their irregularity and their inconstancy I have assigned to them no morphological value, although in sections they often present the appearance of true segmental limits, and are therefore very confusing.

In embryos two days older, segment 2 tapers nearly to a point in the dorsal region while ventrally it is very broad and expands to form the relatively broad infundibulum. Segment 3 is still present and distinctly wedged-shaped although its posterior border has become very faint. Segments 4 and 5 are present as described in Fig. 13. Segment 5 is relatively small and appears compressed between segments 4 and 6. Posterior to the deep constriction (*f*) the five segments of the medulla (*7—11*) are regular and equal in size, and confined to the ventral region of the encephalon.

In embryos 36 days old (Fig. 15) the segments of the medulla are about to disappear. With the lateral expansion of the neural tube they seem to have passed ventrad and are now confined to the floor of the medulla which is covered by a high unsegmented brain-roof. The transverse groove between segments 3 and 4 is absent, and only the posterior commissure in the dorsal region marks the posterior limit of the primary fore-brain. Two or three folds have appeared in the lateral walls of the large infundibulum. These in sections are found to affect both the internal and external surfaces and are thus readily confused with true segmental grooves, but must be given different morphological value. Of the two segments that constitute the mid-brain only the posterior one (segment 5) remains distinct, the anterior one (segment 4) having fused with the posterior segment of the fore-brain. Segment 6, the cerebellum, has become very broad and as in younger specimens, extends to the dorsal surface of the encephalon.

The preceding description justified the following conclusions:

1) The encephalon of *Salmo* is divided into 11 primary segments or joints.
2) The dividing planes between these segments are marked by transverse external an corresponding internal constrictions or grooves.
3) These segments appear very early and antedate the historical divisions known as fore-brain, mid-brain and hind-brain.
4) The latter divisions are not simple, but compound and include a definite number of primary segments as follows:
   The fore-brain includes 3 segments.
   The mid-brain includes 2 segments.
   The hind brain includes 6 segments.
   The anterior segment of the hind-brain represents the cerebellum, the other five constitute the medulla.

B. Encephalic Segments of the Chick.

In order to secure a very close series of embryonic stages, upwards of 700 eggs were incubated and opened between the ages of

15 hours and 5 days. Most of the embryos removed were between 20 and 40 hours.

Beginning observations on embryos 45 hours old, in which the segments of the medulla are unmistakable, and proceeding carefully to earlier stages, I have traced these segments in unbroken continuity back to embryos with one somite. In older stages they have been traced forward to the fourth day of incubation after which they disappear.

The age of embryos has been determined by reference to DUVAL's Atlas d'Embryologie.

a) Embryos with open Neural Grooves (1—6 Somites), Ages 21—25 hours.

When the cephalic mesoderm is dissected away from the neural grooves of embryos with 5$^1/_2$ somites and the specimens studied by reflected light, eleven transverse neural constrictions (Plate 29, Fig. 22 *a—k*), are to be seen which divide the neural axis into 11$^1/_2$ nearly equal segments. Figs. 22 and 23 represent respectively dorsal and lateral views of the same encephalon of an embryo 24 hours old, with 5$^1/_2$ somites, while Fig. 24 represents the encephalon of the same embryo after it has been divided and the inner surface of the left half exposed to view. In the dorsal and lateral views (Figs. 22, 23), the eleven transverse constrictions or grooves can be traced ventrally around the whole neural axis. The neural segments, therefore, include ventral elements as well as dorsal. If Figs. 22 and 23 be examined more closely it will be observed that the 3rd and 5th grooves (*c* and *e*) are deeper than any of the others. In older specimens it is found that these grooves form not only the posterior borders of segments 3 and 5 but also mark the anterior limits respectively of the mid-brain and the hind-brain. While the conventional division of the encephalon into primary fore-brain, mid-brain and hind-brain has a historical value it is to be observed that an earlier segmentation is incorporated into this division as follows: In the fore-brain, three primary segments are included (Figs. 22 and 23 *1—3*); in the mid-brain, two (*4* and *5*) and in the hind-brain, six (*6—11*), or six and one-half if the portion of segment 12 that lies in front of the first somite is added to the latter.

If we now direct our attention to Fig. 24, which represents the encephalon of the same embryo after it has been divided and the inner surface of the left half exposed, we observe, 1) that along the thickened dorsal crest the primary segments are very conspicuous and correspond in number and position to the segments described on the external surface, 2) in the ventral and lateral grooves the dividing lines between segments 3 and 4, and segments 5 and 6, are transverse ridges (*c'* and *e'*), while farther caudad the dividing lines are grooves. The transverse ridge *c'* thus marks the posterior border of the fore-brain, which, as stated above, includes segments 1—3; that portion between the ridges *c'* and *e'* represents the mid-brain and includes the primary segments 4 and 5. It thus appears that the joints or segments on the inner surface of the neural groove correspond in number and position to those observed on the external surface.

Fig. 21 represents the left half of the divided encephalon of an embryo with 3 somites 23 hours old, one hour younger than the embryo just described. The inner surface is exposed to view, showing eleven transverse grooves corresponding to those described in the other specimens, and agreeing in number and position to those on the external surface. From a comparison of Fig. 21 and Fig. 24, it appears that the transverse ridges *c'* and *e'* (Fig. 24), are preceded by transverse grooves. This is also true of the segmental ridges that are present on the inner surface of the hind-brain of older embryos.

I have traced these segments, by dissection through a close series of younger specimens to embryos with one somite (Plate 29, Fig. 16—20). The 11 constrictions are present on both inner and outer surfaces of the open neural groove, and are not only continuous with each other, but appear to fall in the same transverse planes. It should be noted that these segments are constant in number and nearly equal in size, and that they appear earlier in the ontogeny than the historic encephalic divisions, fore-brain, mid-brain and hind-brain. The latter are not strictly segmental divisions and are differently composed, the fore-brain having 3 segments, the mid-brain 2, and the hind-brain 6.

b) Embryos with 6—7 Somites (Ages 25—26 hours).

Figs. 25, 26 and 27 represent different views of the encephalon of an embryo with $6^1/_2$ somites, about $25^1/_2$ hours old. In the dorsal view, Fig. 25, it will be seen that the neural groove has closed in the region of segments three to seven but still remains open both caudad and cephalad. In the dorsal and lateral views, 11 encephalic segments can be counted. At this stage the evagination of the lateral eyes is so advanced that in the dorsal view the three anterior segments can be detected only along the thick dorsal margin (Fig. 25 *1—3*). In the ventral zone these three segments appear better defined (see Fig. 26 *1—3*). The remaining eight segments may be observed in either a dorsal or lateral view. The transverse grooves that mark their anterior and their posterior limits, pass around the neural axis, and in the posterior encephalic region where the neural tube is still open, they become directly continuous with segmental lines that are present on the inner surface of the encephalon, as will appear later from a study of the divided specimens. The developmental history shows that, after the neural groove has closed to form a tube, these identical posterior segments persist and can be recognized as neuromeres of the medulla, so extensively described by other authors in all Vertebrate groups.

In these figures the fore-, mid- and hind-brain divisions are better seen than in the earlier stages but it should be remembered that they are not simple but compound — as this shows clearly in a side view of the encephalon (Fig. 26). The fore-brain has three primary segments (*1—3*); the mid-brain has two (*3—4*), and the hind-brain has six (*5—11*). Fig. 27 represents the encephalon just described after it has been divided and the inner surface of the left half exposed. There are, as in Fig. 24, eleven segments in the thickened dorsal margin (*1—11*). Along this margin the dividing lines between these segments appear as transverse grooves, while in the lateral and ventral region they are continued as transverse ridges or crests. It should be remembered that all these ridges are preceded by transverse grooves. We can thus detect on the inner surface and along the dorsal margin the same number of primary segments as were observed on the external surface.

We have here the first traces of the typical "neuromeres" described by Orr, '87, as follows: "Each neuromere is separated from its neighbor by an external dorso-ventral constriction, and opposite this an internal sharp dorso-ventral ridge." In the description of sections of these segments it will appear that grooves are present at the apices of many of these ridges, and that the ridges are probably produced passively by an intrasegmental lateral expansion of the neural tube.

The optic evagination bears such a close relation to the three anterior neural segments that this description would be incomplete without its developmental history. This evagination is present in embryos with open neural grooves. In the three figures just described

(Figs. 25—27), this evagination is present in the dorsal region of the neural tube and involves the primary segments 1, 2 and 3. In the profile view (Fig. 26), the second segmental groove that forms the dividing line between segments 2 and 3 is restricted to the base of the brain and to the ventral portion of the optic evagination. The latter in this view appears partly divided. In Fig. 23 this groove completely divides the optic evagination; in embryos a little older (Fig. 26), the groove is shortened and affects only the base of the optic expansion, while in still older embryos (Figs. 29, 31), this groove has entirely disappeared.

In embryos with 5 to 7 somites and in favorable specimens, the dorsal portion of segments 4—7 shows a lateral expansion just below the neural ridge (Fig. 26). In the divided embryos of this age these expansions may be detected as faint depressions on the inner aspect of the neural tube (Figs. 24 and 27). Locy, '97, has described these structures as "accessory optic vesicles" and has observed them in favorable undissected embryos of this age and also in sections. The fact that these transient "vesicles" appear as a direct caudad continuation of the optic expansion which itself is primarily divided (see Figs. 23 and 26), coupled with the well known fact that the optic evagination extends at first along the whole length of the primary fore-brain and later retains a union with only the distal portion of this brain, are collectively suggestive of a segmental and multiple origin of the visual organ in the Vertebrate phylum.

In Figs. 28 and 29, that represent two views of the encephalon of a dissected embryo with 7 somites, 26 hours old, the three anterior segments are about to fuse to form one large division, the primary fore-brain. The second transverse groove is confined exclusively to the base of the brain without encroaching upon the ventral portion of the optic evagination as in Fig. 26. The "accessory optic vesicles" have disappeared. In the dorsal view three transverse segmental grooves (*c*, *e* and *g*) are relatively deep.

The portion between the grooves (*c*) and (*e*) represents the mid-brain and includes segments 4 and 5. That portion between the grooves (*e*) and (*g*) includes segments 6 and 7. As will appear later, segment 6 develops into the cerebellum and 7 is the anterior segment of the medulla. We have here a lateral neural expansion, analogous to that observed in the trout (page 17, Figs. 2, 3), which also involved segments 6 and 7. At this age therefore, the distal portion of the encephalon presents three large divisions or vesicles, which it must be remembered are not simple but compound.

c) Embryos with 7—20 Somites (Ages 27–40 hours).

After the complete closure of the neural groove in the cephalic region all evidence of metamerism in the primary fore-brain has disappeared, and the distal portion of the neural axis has thus the appearance of a single simple vesicle. The optic evaginations are gradually being confined to the anterior portion of the encephalon. In a dorsal view of an embryo with 11 somites 29 hours old (Fig. 30), the three large distal encephalic vesicles appear unsegmented but, in the profile view (Fig. 31) the same encephalon shows, on its external surface, a transverse groove that divides the middle vesicle or mid-brain into two segments (segments 4 and 5), and also a second groove that divides the vesicles caudad to this into two segments (segments 6 and 7). Both of these grooves are restricted to the lateral and ventral portions of the encephalon. As mentioned in the description of Figs. 28 and 29, segment number *6* represents the cerebellum and number *7* is the anterior segment of the medulla. The remaining segments of the medulla (*8—11*) have become very distinct and their dividing lines pass entirely around the neural axis.

In embryos with 14 somites, 33 hours old (Figs. 32 and 33), the mid-brain is unsegmented. The groove that forms the dividing line between segments 6 and 7 (Fig. 33), has almost disappeared. In later stages, however, this constriction becomes again distinct. At this age a transverse constriction (*r*) is present in the dorsal region of the primary fore-brain, just dorsal to the optic vesicle. This is a permanent constriction that ultimately divides the primary fore-brain into the prosencephalon and thalamencephalon.

The five segments of the medulla (*7—11*), are more sharply defined than in younger specimens. The auditory vesicle occupies an intersegmental position between segments 10 and 11 (Fig. 32 *au.vs*). Up to this time the segments of the hind-brain have been equal in size and alike in form. As observed in Fig. 33, segment 9, which is connected with the 7th and 8th cranial nerves, has now become wedge-shaped with the apex turned dorsad and ever after this affords an anatomical land mark. The two adjacent segments are modified in a reciprocal manner. This condition prevails till the segments ultimately disappear.

Figs. 34 and 35 represent ventral and profile views of the encephalon of an embryo with 16 somites 33 hours old. The transverse groove that separates segment 6 from segment 7 has become more distinct, otherwise the segmental characteristics are the same as those described in Figs. 32 and 33.

In embryos with 20 somites three hours older a very marked change has occurred in the region of the hind-brain. In the dorsal view (Fig. 36) the segments of the medulla have expanded laterally, especially segment 8 which now represents the widest part of the hind-brain. The dorsal surface of this region is smooth and unsegmented. Of the seven transverse segmental grooves that are now present, only two (*c* and *e*) completely encircle the brain. These, as observed before, mark the anterior and the posterior limits of the mid-brain.

d) Embryos 40 to 100 hours old.

Figs. 37 and 38, Plate 3, represent two views of the encephalon of an embryo 43 hours old. The encephalon has partly turned upon its left side. The expanded condition of the medulla reveals the presence of a broad cavity, the 4th ventricle, lying beneath a thin unsegmented roof. The six segments of the medulla present the same characteristics as previously described in Fig. 36. When the embryo has turned completely upon its left side (Fig. 39), the position of the 4th ventricle with its thin unsegmented roof is more clearly defined. Segment 6, the cerebellum, has broadened and from this time on continues to differentiate from the other five segments of the hind-brain.

In embryos 50 hours old, the segmentation of the medulla is practically unchanged (Fig. 40). The cavity of the 4th ventricle has expanded laterally and its thin unsegmented roof has increased in extent. A transverse dorsal groove (*s*) has appeared dividing the thalamencephalon into two nearly equal divisions, and at this age therefore three distinct divisions can be recognized in the primary fore-brain, viz., a distal portion, the cerebrum and two proximal portions that represent the two divisions of the 'tween brain.

The segmental condition just described remains practically unchanged in all essential features during the entire third day of incubation. Fig. 40 may therefore very well represent this period.

During the last half of the fourth day of incubation the segmentation of the medulla very rapidly grows indistinct and ultimately disappears. Fig. 41 represents the encephalon of an embryo 80 hours old. The segmental grooves of the medulla at this age terminate dorsally in a longitudinal lateral ridge, along which the thin unsegmented roof of the 4th ventricle it attached. The cerebellum (segment 6), forms the anterior expanded wall of the 4th ventricle just as in trout embryos 30 days old. The thalamencephalon is divided into two portions by a dorsal constriction (*s*) that made its appearance during the third day of incubation. They very late appearance of these divisions, and the fact that they are produced by a dorsal constriction render it highly improbable that they have the same morphological value as the early encephalic segments.

From this description it appears that the encephalic segments of the chick and the trout differ only in one detail. In the trout the dividing lines between the segments form grooves on both the external and the internal surfaces. In the chick after the neural groove has closed to form a tube, the dividing lines on the inner surfaces of the medulla are represented by transverse ridges. It is to be remembered, however, that each ridge is preceded by a transverse groove, and that many of the ridges have at their apices traces of this groove, as the description of sections will show.

With this exception the conclusions reached from the study of the encephalic segments of the chick are identical with those reached from a study of the trout (see page 24).

C. Study of Sections, Chick and Trout.

The value of making dissections even of the smallest embryos can scarcely be overestimated. The segmental furrows can be identified with greater certainty on the dissected embryos than by means of sections. The surface observations, also, serve as a check upon the sections and vice versa. As my series of sections agree completely with the surface studies, the following description will be brief and limited to the most typical sections.

Fig. 42, Plate 30, represents a parasagittal section through the cephalic region of a trout embryo 22 days old, and should be compared with the divided encephalon of the same age (Fig. 11, Plate 1). Eleven encephalic segments are present (*1—11*). These are not only separated from each other by dorsal and ventral constrictions but by the transverse narrow septa, which, as Orr has stated, may be nothing else than parts of cell walls "which are made conspicuous by lying in a straight line". The feature of chief interest is five segments in fore- and mid-brain, similar to those in the medulla. Modification of the most anterior segments have not progressed far enough to make them different in any marked way from those of the medulla. Segment 1 is elliptical, and represents the anterior end of the neural axis. Segment 2 is wedge-shaped and has its broad end extended ventrally to form the infundibulum (*inf*). The dividing lines between 3, 4 and 5, could be detected in this section in the ventral region and the series of sections confirm the description given of these segments in surface studies. The five segments of the medulla (*7*—*11*) and the cerebellum (segment 6), are well defined. Just ventrad to the latter is the deep dorsal groove (*f*) observed in both the divided and the dissected specimens.

While the segments of the primary fore-brain and the mid-brain are detected with difficulty in sagittal sections, they are more clearly defined in horizontal sections. Fig. 43 represents a section nearly horizontal through this region, the section passing at an angle such as to intersect the right eye and a point just dorsal to the left eye. This section is made from a trout embryo 26 days old and should be compared with the divided embryo of the same age (Fig. 13). In this as in the sagittal section the evidence of the jointed character of the fore- and mid-brain is very clear. Since the section passes through the dorsal region segment 2 is very narrow and segment 3 very broad. A section through the ventral region would just reverse this order, as these segments are reciprocally wedged-shaped. It is observed that a secondary depression is present in segment 5 and also a median depression in segment 3. These depressions, if sections alone were studied, would lead to error in counting the number of encephalic segments, a mistake that is checked by the study of a series of divided embryos.

Fig. 44 represents a horizontal section through the anterior portion of a chick embryo with four somites and with open neural groove. The encephalic mesoblast is very loose and presents no satisfactory evidence of segmentation. There is an irregular grouping of its cells which makes loose clusters of cells that agree in number with the segments. The neural groove, however, is distinctly divided into segments by a series of external and internal constrictions. These segments, on the right and left sides, are directly opposite each other and furthermore each external constriction has a corresponding internal depression that lies in the same transverse plane. No "internal crests" or "ridges" are present as described in older stages of the chick embryo.

As soon as the neural groove closes, internal transverse crests appear, as represented in Fig. 45. This figure shows a horizontal section through the left half of the neural segments, 6—9 of a chick embryo 42 hours old. At this age all the characteristics of a typical "neuromere" as described by Orr are present.

1) "Each neuromere is separated from its neighbor by an external dorso-ventral constriction and opposite this an internal sharp dorso-ventral ridge, — so that each neuromere (i. e. one lateral half of each) appears as a small arc of a circle.

2) The elongated cells are placed radially to the inner curved surface of the neuromere.

3) The nuclei are generally nearer the outer surface and approach the inner surface only towards the apex of the ridge.

4) On the line between the apex of the internal ridge and the pit of the external depression, the cells of adjoining neuromeres are crowded together, though the cells of one neuromere do not extend into another neuromere.

This definition of adjacent neuromeres presents in some sections the appearance of a septum extending from the pit of the external depression to the summit of the internal ridge" (Orr, '87, p. 335).

In addition to the above characteristics I find a transverse groove (*g'* and *f'*, Fig. 45), at the apex of many of the internal ridges or crests. The internal transverse grooves described in embryos with open neural grooves have thus become elevated, in the medulla of the chick, and occupy a position at the apices of the internal transverse ridges. A discussion of this observation appears in another portion of this contribution (page 35).

Fig. 46 represents a horizontal section of the medulla of a trout embryo 27 days old, a stage when the neural segments are highly developed. It will be observed that the dividing lines between segments are represented by external and internal transverse grooves that lie in nearly the same transverse plane. The cells are elongated and arranged radially to the internal surface. The nuclei are large and well supplied with chromatin. The septa that separate adjacent segments are usually very distinct and, as Orr has stated, may be nothing more than the walls of adjacent cells that are placed in straight lines. The histological condition of the neural segments of the chick embryo (Fig. 45) is identical with the description given above.

In younger embryonic stages of the chick and the trout, the histology is very simple. The radial arrangement of cells is absent. The nuclei do not recede intrasegmentally from the inner surface of the brain, but are very evenly distributed. In these stages the only criteria, by which I have counted neural segments, are external and corresponding internal transverse constrictions or grooves.

The segmental value of the cranial nerves, while important, has so frequently been shown to be deceptive and misleading (McClure, '89; Minot, '92; Locy, '95, and Neal, '98), that it is unnecessary here to repeat this evidence. While recognizing that the deep origin of the cranial nerves is the important criterion, I wish here merely to locate their union with the brain in order to establish more accurately the identity of the individual neuromeres, as described here, with those of other observers. I have found the same nerve connection in the trout as in the chick. The following description therefore, applies to either type.

The olfactory and optic nerves are connected respectively with the first and second segments. From the ventral region of the mid-brain and the posterior portion of segment 4 the fibres of the oculomotor nerves (Fig. 21) pass ventrally and laterally, close to the ciliary ganglion and innervate the fundament of the muscles of the eye.

The fourth pair of nerves are connected with the dorsal and posterior region of the mid-brain or segment 5.

Laterally and in the dorsal portion of segment 6, the fibres of the anterior root of the Trigeminus emerge and pass to the Gasserian ganglion (Fig. 48 *ant. rt. V*).

From segment 7 the main fibres of the trigeminal nerve pass cephalad to the Gasserian ganglion (Fig. 49 and 50).

Segment 8 has no nerve connection.

Segment 9 gives rise to the fibres of the seventh and eighth pair of nerves (Fig. 49 and 50 *VII* and *VIII*).

Segment 11 is connected with the fibres of the ninth pair of cranial nerves (Fig. 50).

I also confirm the observation of Miss Platt, Hoffmann and Locy that the origin of cranial nerves is from the external depressions, between adjacent segments.

III. General Considerations.

Identifications of Neural Segments.

In discussing metamerism of the head it should be borne in mind that the neural segmentation is merely an expression of the general segmentation of the body. This primary division into joints is not confined to the neural axis, but as Locy pointed out, it involves the rest of the germ layers, and the question of primary segments is thus wider than that of metamerism of the head. It is a general embryonic segmentation, most readily seen in the neural axis which is the seat of most active growth in these early stages.

In describing neural segments there has been more or less confusion and for purposes of clearness it becomes necessary to inquire into the means of identifying segments. In the preceding pages the term "neural segment" has been used because it is purely descriptive and does not imply any morphological interpretation. It simply recognizes the fact that the neural axis is divided into a series of joints or segments.

As boundaries of encephalic segments in trout and chick embryos, I have used external and corresponding internal transverse constrictions or grooves. These constrictions are uniform in number and position in early embryonic stages, and divide the encephalon of the neural axis into what I believe to be morphologically identical segments or joints. In the early stages these grooves encircle the encephalon but in later stages the primary segmentation is confined only to its base and lateral walls, owing to the neural expansion and the appearance in the dorsal region of a thin roof. It should be remembered 1) that in the position occupied by the 3rd, 5th and 6th segmental grooves, deep external constrictions appear that form the posterior limits respectively of the fore-brain, mid-brain and cerebellum, and 2) that all the primitive grooves vanish during embryonic growth, those of the fore-brain first and those of the mid-brain second and lastly those of the hind-brain. In the chick when the neural folds close to form the neural tube, the walls of the latter expand, not uniformly, but intrasegmentally, and the position of the internal grooves is thus passively elevated upon crests (see Fig. 45 *g'*, *f'*).

Much importance has been attached to the definition given by Orr of a typical neuromere (McClure, Waters, Neal and others). It will be of advantage to make a few observations upon the morphological value of the factors used in this definition. I have observed all five characteristics considered by Orr as fundamental. Regarding the 1st, viz., that "each neuromere is separated from its neighbor by an external dorso-ventral constriction and opposite this an internal sharp dorso-ventral ridge", it should be remembered that the "dorso-ventral ridge" is absent in Teleosts, and in the chick it has at its apex a groove which arises ontogenetically before the ridge. It seems to me therefore that the ridge is a secondary modification. 2) The radial arrangement of cells mentioned by **Orr** is present only during the stages of intrasegmental expansion of the neural walls to which may be attributed the radial cytological condition. At least prior to the expansion a radial arrangememt is absent. 3) That the nuclei should be "nearer the outer surface and approach the inner surface only toward the apex of the ridge" is a condition that would, it seems to me, also very naturally follow a neural intrasegmental expansion. This nuclear arrangement is present only in late segmental stages. While in later stages I find the three characteristics just mentioned, there are present in early embryonic stages only the two following criteria given by **Orr**, viz., 4) "The constrictions are exactly opposite on each side of the brain" to which I would add: and in the same transverse plane as the internal grooves with which they are continuous, and 5) "On the line between the apex of the internal ridge and the pit of the external depression the cells of the adjoining neuromeres are crowded together though the cells of one neuromere do not extend into another neuromere". To cover the case in Teleosts where the rudimentary ridge is absent it would be necessary to modify the statement as follows: The cells of the adjoining neuromeres are usually crowded together though the cells of one neuromere at no time extend into another neuromere. To this should also be added **Orr**'s statement that "adjacent neuromeres present in some sections the appearance of a septum extending from the pit of the external depression to the summit of the internal ridge".

Neural Segments in Teleosts.

It is a pertinent question how far the description of the neural segments in Teleosts, as presented in this contribution, confirms the observations of other authors and what new facts have been considered. To answer it attention must be directed to the literature. The first recorded observation upon neural segments in Teleosts, known to me, is by **Dohrn** in his Ursprung der Wirbelthiere und das Princip des Functionswechsels, 1875, where he says (quoted from **Hoffmann**, in: **Bronn**, Class. Ord. Thierreich, V. 6, Abtheil. 3, p. 1967): "If one observes the first stages of the embryonic formation of a Vertebrate, for instance, a bony fish, one can scarcely escape the idea that this is an animal made up of a large number of segments. The so-called primitive vertebræ appear [as so many segments or metameres and one sees plainly from 8 to 9 segments in the region of the fourth ventricle of the neural tube." (Author's translation.)

Kupffer, '86, in a brief paper (p. 469—476) reports finding five segments in the hind-brain and three in the mid-brain of the trout. As to the mid-brain and segmental criteria, he says: "Sagittal sections through each embryo show three pair of segments in the vicinity of the mid-brain that resemble those of the medulla oblongata, that is, they are little swellings upon the floor and the sides of the medulla, separated from one another by transverse grooves." (Author's translation.)

Reighard, '90, figures and describes six segments in the hind-brain of *Stizostedion vitreum* that in every way are identical with the segments of this region in the trout.

In my paper on The Development of the Epiphysis in Coregonus albus (Hill, '91), I figure and briefly describe eleven segments in the encephalon of the white fish embryo 7 mm long, 60 days old. Five of these are located in the primary fore- and mid-brains.

The only paper dealing especially with this subject is that of Waters, '92, who finds 11 segments in the encephalon of the cod. He assigns a segmental value to the olfactory nerves and says: "The region of the brain-wall giving rise to them shows markedly the characteristics of a true neuromere as defined by Orr and is, I think, the first or olfactory neuromere" (in: Quart. Jour. micr. Soc., V. 3, p. 463). Regarding the encephalon just back of this olfactory neuromere he writes: "While none of my cod sections give any reliable evidence of a neuromere at this point I will show that in *Amblystoma* there is certainly a second neuromere and that the optic diverticula hold a curiously significant and close relation to it" (p. 464). His direct evidence of a third neuromere in the primary fore-brain of the cod is equally incomplete as the following quotation shows: "The distance from the posterior commissure to the termination of the second neuromere is about one-third the entire length from before backward to this point." . . . "From the fact that there is just sufficient room at this point for another neuromere and that in *Amblystoma* I have been able more satisfactorily to prove its existence, I have called this the third neuromere, thus making the fore-brain contain three neuromeres" (p. 464).

In the region of the mid-brain Waters finds "two well marked convolutions of the brain wall. These constrictions are slightly smaller than those of the fore-brain and rather more semicircular in shape" (p. 465). He also finds that the "radial arrangement of cells is present". There can be but little doubt that the two segments described by WATERS in the mid-brain of the cod are identical with the two mid-brain segments of the trout as described in this contribution. From a study of the figures by WATERS, I am inclined to believe the author considered the internal transverse encephalic grooves as intrasegmental in position when according to my interpretation they are intersegmental and occupy the same morphological position as the transverse internal crests of the chick encephalon (see page 26). So far as number of encephalic segments are concerned and their distribution, my observations on the trout agree with WATERS.

While my description agrees with WATERS as to number of segments, they serve to point out certain discrepancies. His identification of neuromeres in the fore-brain is vague and his enumeration is based on analogy and largely on inference. The descriptions of neural segments in Teleosts in front of the medulla, as given in this paper are, I believe, the only ones based entirely on direct observation of the segmental structures themselves.

The condition of the neural axis in front of the cerebellum is especially well shown in the earliest stages and the existence of five segments in fore- and mid-brains is made evident. This is the first satisfactory evidence of this condition that we have in the Teleosts, LOCY has shown the same in Elasmobranchs (*Acanthias*) and the chick. At least, this region very early shows joints like those in the medulla. They are formed in the same way, resemble them in all essential particulars. It seems to me to be straining the point to deny that these are segments when segmental value is assigned to the homologous segments in the medullary region.

Incidentally these observations show something about the probable morphological front of the brain. HERRICK, '91, writes: "The morphological front of the brain cannot be beyond the infundibulum" (in: Journ. comp. Neurol., p. 168). HIS, '93, believes the cephalad extremity of the neural tube in chick embryos is turned ventro-caudad and the morphological front of the neural axis therefore is in the vicinity of the recessus infundibuli, while KUPFFER sums up the evidence as follows: "Is the neural tube open anteriorly then the neural axis terminates in this opening; is the end of the tube bent, then the neural axis follows this curve. I consider therefore, that the encephalic axis terminates in the neuropore" (in: Verh. anat. Ges., 1893, p. 101). (Author's translation.)

As shown above (Figs. 10—15) in *Salmo* the infundibulum is a ventro-caudad expansion of the second cephalic segment. The recessus infundibuli is an expansion of the neural cavity of this segment. The morphological front of the brain lies cephalad to this expansion and is represented by segment 1. To this segment the fibres of the olfactory nerves pass and the evidence would seem to be clear that the latter constitutes the first pair of cranial nerves (contra VAN WIJHE). The optic nerves on the other hand are connected with segment 2 (see pages 17 and 21, Figs. 3 and 10), and thus becomes the second pair of cranial nerves.

In the chick the primary neural segmentation in the fore-brain has disappeared when the optic nerves are produced and the infundibulum evaginated. The chick therefore is a less favorable type than the trout in which to study this relation.

Neural Segments in the Chick.

It is a noteworthy fact that no recent conflicting observations are recorded regarding the segments of the medulla of the embryonic chick. BÉRANECK, '87, PLATT, '89, McCLURE, '90, ZIMMERMANN, '91, LOCY, '95, all affirm that caudad to the cerebellum there are five encephalic segments present in all chick embryos during the third day of incubation. It is the region in front of the cerebellum that constitutes the disputed territory. Miss PLATT, '89, considers that region made up of but one segment, the primary fore-brain and mid-brain. The cerebellum constitutes the second segment, making a total of seven encephalomeres of equal morphological value in front of the first protovertebra. She offers as evidence in support of this conclusion the presence of external transverse encephalic constrictions and corresponding internal folds.

McCLURE, '90, uses histological conditions as well as external neural constrictions as criteria for encephalic segments. In this way he finds at least two segments in the primary fore-brain and two in the mid-brain of chicks in the third and fourth days of incubation. The cerebellum constitutes his fifth neuromere which with the five of the medulla make a total of at least ten encephalic joints or segments. I have studied McCLURE's figures and reviewed his contribution with much care. If I understand him correctly his neuromeres I and II are restricted to the thalamencephalon. He does not mention the prosencephalon cephalad to his neuromere I, from which I infer he does not include this portion in the true segmental region.

If my interpretation of McClure's position is correct, it seems to me he has described the conditions that are represented in my Figs. 40 and 41. At this stage the thalamencephalon is clearly divided into two segments by the presence of a dorso-lateral invagination (s) in which the fibres of the posterior commissure develop. The fact that this invagination begins as a dorsal constriction, and that its appearance is ontogenetically late, after much specialization has occurred and long after the other segmental constrictions have appeared, is strong evidence that this invagination has a very different morphological value than the constrictions of true encephalic segments.

Regarding the presence of two neuromeres in the mid-brain of chick embryos during the third day of incubation, McClure admits that the evidence is very problematic. The mid-brain, he says (p. 48), "has the appearance of being an enlarged neuromere".... "Its cell structure is radial but its nuclear arrangement does not conform to a typical neuromere except that at its anterior and posterior limits the cells are crowded together and do not enter the adjoining structure." In conclusion he writes (p. 49): "Taking into consideration the size of the mid-brain neuromere in comparison with the remaining neuromeres of the brain as well as its neuromeric characteristics, also the fact that two nerves arise from it which are probably either two segental nerves or parts of the same, also the investigations of Kupffer, previously mentioned, in which he states that he found at least eight segments in the hind- and mid-brains of the Trout and Salamander, there can be little doubt left but that the mid-brain originally consisted of at least two neuromeres and that in all probability the III and IV nerves were segmental nerves of these neuromeres respectively."

I have studied the mid-brain of chick embryos with much care by the method of sections and dissection. In embryos thirty hours and older I find no evidence of segmental division excepting the presence of the oculomotor and trochlear nerves whose fibres connect with the mid-brain. In young embryos, however, transverse grooves divide the mid-brain into two segments which, according to the descriptive portion of this contribution, constitute encephalic segments 4 and 5 (Figs. 25—30).

Regarding the 13 encephalomeres that Zimmermann, '91, affirms of embryos of all higher Vertebrates, I have but little to say, as the author in his brief paper does not state the criteria used in determining this number. From the fact that he thinks, for some reasons, segmentation is retarded cephalad to the cerebellum, it seems probable that he has also, as McClure, observed the late secondary division that appears in the primary fore-brain, as represented in Figs. 40 and 41.

Locy, '95, from a surface study of undissected chick embryos has observed $11^1/_2$ segments in the dorsal region of the neural groove cephalad to the first formed somites. My description of the neural axis of the dissected embryonic chick as embodied in this paper, is a verification of these observations. I am also indebted to Dr. Locy for placing at my disposal an unpublished manuscript with figures, prepared some years ago by Mr. F. A. Hayner, one of his students, who for more than a year made a close study of the early neural segmentation in the embryonic chick finding at the close of the first day of incubation $11^1/_2$ neural segments in front of the first formed protovertebra.

According to my observations there is complete agreement as to the number and position of the neural segments in front of the cerebellum in the trout and the chick. The fore-brain has three and the mid-brain has two. These segments do not differ in the earliest stages in any essential features from those of the medulla. They are present in the same early embryonic stages as those of the medulla but owing to the rapid changes that take place in the anterior cephalic region they disappear very early, those of the fore-brain first and those of the mid-brain second. They antedate the historic divisions, fore- and mid-brains, and precede even the optic evaginations. In short they represent a phylogenetic condition older than the organs, possibly even older than the phylogeny of the neural axis.

Value of Various Segmental Criteria.

a) Mesomeres. My observations were naturally directed to the joints of the neural axis because, in the head region, they afford the most evident traces of joints or segments to be found; but, the mesoblast of the head region was also subjected to close scrutiny. It was hoped that at least some trace of the head cavities that are present in the cephalic mesoderm of the shark, would be found in the Teleost embryo. The study of numerous sections of both chick and trout embryos has given no positive evidence of the presence of such cavities. The loose and somewhat scattered mesoderm occasionally presents a grouping of cells that might be interpreted of segmental significance but otherwise this tissue remains unbroken.

The study of cephalic mesomeres has led to greater divergence of opinions and more conflicting views than is generally supposed. In Elasmobranchs, the only group in which their developmental history has been traced, there is no consensus of opinion as to their origin, number, and morphological values. Van Wijhe, Dohrn, Killian, Miss Platt, hold that they are all fundamental segmental divisions of the cœlomic cavity. Gegenbaur, Sedgwick, Rabl, Sewertzoff maintain that some of them probably represent gill clefts and other divisions of the cœlomic cavity. In the Elasmobranchs, in the pre-otic region, from 3 to 14 segments are recorded (Rabl, '92, and Dohrn, '90). Moreover, some observers conclude that certain cephalic mesomeres have disappeared in phylogenetic history (Sedgwick), while others claim a fusion of segments has taken place, and still others maintain that primary segments have subdivided and in this way have produced a larger number of "head-cavities" than were originally present in the ancestral Vertebrates.

In sequence of time they are said to develop from before, backwards. Gegenbaur, '87, insists that we should carefully observe a distinction between palingenetic (primary) and cœnogenetic (secondary) somites. This is philosophical and supported by fact of development. It has been generally adopted (Kastschenko, '88, Sewertzoff, '95, Hoffmann, '97). The segmental divisions of the mesoblast has been shown to begin in the region of the auditory vesicle and develop backwards. This gives us the post-otic or palingenetic segments. The mesoblast in front of the auditory capsule is afterwards divided into segments designated as pre-otic or cœnogenetic.

The cœnogenetic segments are found to differ in form, size, histological conditions as well as time of development. Some of these segments are solid, while most of them show a cavity. They may be partially or completely separated from the adjacent ones, united or separated ventrally, and also occupy a lateral or a ventral position with reference to the neural axis.

Since the study of their developmental history, in the Elasmobranchs, has led to such a variety of views, their morphological interpretations vary in like degree and this weakens their value as segmental criteria. Some authors assign to all cephalic mesomeres a fundamental segmental value. Some hold the post-otic only have this value, while the pre-otic are interpreted as mechanical structures or evaginations correlated with the gill clefts.

The recorded observations on the cephalic mesomeres in other

Vertebrates, are so limited that we have little knowledge regarding their presence or possible conditions. The controversies, therefore, are almost exclusively confined to the observations that have been recorded upon the mesomeres of Elasmobranch embryos.

While it must be admitted that the cephalic mesoderm may carry the evidence of a primitive metamerism, it seems to me that all the observations go to show that there is too little uniformity about the divisions of this tissue to make it a favorable structure for determining the number and relationship of cephalic segments.

b) Branchiomeres. The weakness of branchiomeres as clues to the original segmentation of the head has been well stated by Minot, '92: "The relation of the nerves to the segments (myotomes and neuromeres) are primitive; the relations to the branchial arches and gill-clefts are secondary. Indeed we must assume that the Vertebrates had segmental ancestors, who acquired gill-clefts, segments being phylogenetically much older than gill-clefts. The ancestral nerves were adapted to gill-clefts and we may some day know the history of that adaptation and the modifications consequent upon it. At present we can only say that, contrary to the assumption which has prevailed for twenty years, the gill-clefts are not segmental and therefore the branchial nerves are not in segmental order." (Human Embryology, p. 636.)

c) Neural Segments. The case seems to stand somewhat better for the neural segments. Those of the medulla are accepted by most morphologists as representing true joints or segments. It is those of the fore- and mid-brain regions whose presence and segmental value is questioned. The identity of those of the medulla and their relation to nerves is well established in all the Vertebrate groups from fishes to mammals. Unfortunately, but few observers have attempted to trace their complete history. The observations have been confined almost exclusively to late stages and the neural segments, therefore, have come to be looked upon as structures that follow rather than precede the segmental divisions of the mesoblast. Locy was the first to observe the early stages of the neural segments. He found that they could be traced back to stages that antedate the formation of mesomeres. The significant fact is that Locy traced them, as his sketches show, from their earliest appearance through the stages with an open, a closing, and a closed neural groove, and identified those of the medulla with the neuromeres of other authors.

Neal, '98, found segmental divisions in early stages of sharks as described by **Locy**, but denies their segmental importance. He was unable to find them in stages immediately preceding closure of the neural groove, and bases a conclusion on this negative evidence, together with their irregularity, that the early segments have no connection with those of later stages. The evidence in Teleosts and chicks is very clear as to their unbroken continuity, and I know also from my own observation that corresponding segments are present in *Acanthias* where **Neal** failed to find them. The view first advanced by **Locy** that these early segments are the same as the neuromeres observed in the medulla from 1828 onwards, receives support from the work recorded above. And it also strengthens the contention that in the early stages a jointed condition is present in the anterior portion of the neural axis that agrees in all essential features with that observed at the same time in the region of the medulla.

The anterior segments precede the large divisions known as fore-, mid- and hind-brains. The failure to recognize this fact has led to confusion and conflicting reports as to the segments in front of the cerebellum, notably these larger divisions have, from time to time, been made homologous with the segmental divisions of the medulla. The fact that these larger divisions later subdivide, before the segments of the medulla have disappeared, has led to the erroneous view that the fore- and mid-brains are morphologically equivalent to the segments of the medulla (**Neal** and Miss **Platt**).

As appears above (page 29, Figs. 32—40 *r*) the primary fore-brain, in chick embryos in later stages, is divided into prosencephalon and thalamencephalon by a dorsal constriction that is very different from the transverse grooves that separate adjacent segments in the medulla. In still older stages another transverse dorsal constriction (*s*) appears which divides the thalamencephalon. To these divisions **Waters** and **Zimmermann** appear to have assigned the same segmental value as to the segments of the medulla. It seems to me this is clearly an error as is shown not only by the late appearance of these anterior divisions, but, also, by the developmental history of the dorsal grooves that produce these divisions (see page 29—30). **Herrick** very appropriately writes: "It is scarcely legitimate to count dorsal diverticles like those of the fore-brain with ventral expansions like those of the mid-brain. **Waters** and others seem to have made this mistake" (in: Journ. comp. Neurol., 1892, p. 168).

Since the head is a segmental structure, how may the history of its segments be read? The mesoblastic divisions (head cavities) have been found only in a few Vertebrates (Elasmobranchs, Amphibia and Reptiles), and in Elasmobranchs, the only group in which their developmental history has been described, the authors who have given the subject the most critical study report conflicting and contradictory views. On the other hand, neural segments of acknowledged morphological value have been observed in the medulla by many authors in all the vertebrate groups. These segments can be traced to very early stages before the fore-, mid- and hind-brains have appeared, or mesomeres have developed. In these early stages the neural segments are constant in number and identical in form, but owing to the rapid changes that take place in the anterior portion of the neural axis, the anterior encephalic segments disappear before those of the medulla.

Summary.

In Teleost an chick embryos the encephalic portion of the neural axis is divided into similar joints or segments which in early stages are present in the region of fore- and mid-brain — secondary modification in the anterior encephalic region of the chick soon obliterates all traces of primitive segments, but the original joints persist for some time in the medulla which is less modified. In the Teleosts the segments in front of the medulla are less transient than those of the chick.

In the medulla the original joints persist for some time. Secondary expansions of the mid-brain and fore-brain, arising after the primary joints of this region fade away, have been mistaken for primary segmental divisions, and made co-ordinate with the persisting primary segments of he medulla which are in realty identical with the first formed segments in the anterior brain region.

The three anterior segments represent the region of the fore-brain, the next two the region of the mid-brain. These five segments differ in no essential feature from the segments of the medulla.

The sixth segment forms the cerebellum, and the seventh to eleventh, inclusive, represent the medulla, making a total of eleven encephalic segments. These segments are constantly and normally present in the early stages of all the embryos examined.

Bibliography.

Ahlborn, F., '84a, Ueber die Segmentation des Wirbelthierkörpers, in: Z. wiss. Zool., V. 40, p. 309—337.

v. Baer, K. E., '28, Ueber Entwicklungsgeschichte der Thiere. Theil I. Königsberg. XXII + 271 pp., 3 Taf.

Balfour, F. M., '78, A monograph on the development of Elasmobranch Fishes, London, XI + 295 pp., 20 plates.

— '81, A treatise on comparative embryology, London, V. 2.

Beard, J., '85, The system of branchial sense organs and their associated ganglia in Ichthyopsida. A contribution to the ancestral history of Vertebrates, in: Quart. J. micr. Sc., V. 26, p. 95—156, tab. 8—10.

Béraneck, E., '87, Etude sur les replis médullaires du poulet, in: Recueil Zool. Suisse, V. 4, No. 2, p. 305—364, tab. 14.

Bischoff, T. L. W., '42, Entwicklungsgeschichte der Säugethiere und des Menschen, Leipzig, XIV + 575 pp.

Burckhardt, R., '93, Die Homologien des Zwischenhirndaches und ihre Bedeutung für die Morphologie des Hirns bei niederen Vertebraten, in: Anat. Anz., V. 9, p. 152—155, 1 Fig.

— '94, Der Bauplan des Wirbelthiergehirns, in: Morph. Arb., V. 4, Heft 2, p. 131—150, tab. 8.

Cajal, Ramón y, '94, Les nouvelles idées sur la structure du système nerveux chez l'homme et chez les Vertébrés, in: Rev. gén. Sc. pures et appliquées, Année 5, p. 141—153.

Dohrn, A., '75, Der Ursprung der Wirbelthiere und das Princip des Functionswechsels. Genealogische Skizzen, Leipzig, XV + 87 pp.

— '90, Bemerkungen über den neuesten Versuch einer Lösung des Wirbelthierkopf-Problems, in: Anat. Anz., Jg. 5, p. 53—64, 78—85.

— '90a, Studien u. s. w. XV. Neue Grundlagen zur Beurtheilung der Metamerie des Kopfes, in: Mitth. zool. Stat. Neapel, V. 9, p. 330—434, tab. 14, 15.

Dursy, E., '69, Zur Entwicklungsgeschichte des Kopfes des Menschen und der höhern Wirbelthiere, Tübingen, XII + 232 pp. und Atlas, 9 Taf.

Foster, H., and Balfour, F. M., '74, The elements of embryology, London, XIX + 272 pp., 71 figs.

Froriep, A., '91, Entwicklungsgeschichte des Kopfes, in: Anat. Hefte, Abth. 2, Ergebn. Anat. Entw., V. 1, p. 561—605.

— '92, Zur Frage der sogenannten Neuromerie, in: Verh. anat. Ges., V. 6, p. 162—167.

— '93, Entwicklungsgeschichte des Kopfes, in: Anat. Hefte, Abth. 2, Ergebn. Anat. Entw., V. 3, p. 391—459.

Gegenbaur, C., '87, Die Metamerie des Kopfes und die Wirbeltheorie des Kopfskelets, in: Morph. Jahrb., V. 13, Heft 1, p. 1—114.

Goette, A., '75, Die Entwicklungsgeschichte der Unke (Bombinator igneus) als Grundlage einer vergleichenden Morphologie der Wirbelthiere, Leipzig, VIII + 964 pp. und Atlas (1874), 22 Taf., fol.

Goronowitsch, N., '92, Die axiale und die laterale (A. Goette) Kopfmetamerie der Vögelembryonen. Die Rolle der sog. „Ganglienleisten“ im Aufbaue der Nervenstämme, in: Anat. Anz., V. 7, p. 454—464.

— '98, Untersuchungen über die Entwicklung der sog. „Ganglienleisten“ im Kopfe der Vögelembryonen, in: Morph. Jahrb., V. 20, p. 187—259, tab. 8—11.

Hatschek, B., '92, Die Metamerie des Amphioxus und des Ammocoetes, in: Verh. anat. Ges., V. 6, p. 136—161, 11 Fig.

— '93, Zur Metamerie der Wirbelthiere, in: Anat. Anz., V. 8, p. 89—91.

Herrick, C. L., '92, Embryological notes on the brain of the Snake, in: J. comp. Neurol., V. 2, p. 160—176, tab. 15—19.

Hill, Chas., '91, Development of the epiphysis in Coregonus albus, in: J. Morph., V. 5, p. 503—510.

— '94, The epiphysis of Teleosts and Amia, ibid. V. 9, p. 237—266, 2 pls.

His, W., '93, Ueber das frontale Ende und über die natürliche Eintheilung des Gehirnrohres, in: Verh. anat. Ges., V. 7, p. 95—99.

Hoffmann, C. K., '85, Weitere Untersuchungen zur Entwicklungsgeschichte der Reptilien, in: Morph. Jahrb., V. 11, p. 176—219, tab. 10—12, 1 Fig.

— '89, Ueber die Metamerie des Nachhirns und Hinterhirns und ihre Beziehung zu den segmentalen Kopfnerven bei Reptilienembryonen, in: Zool. Anz., Jg. 12, p. 337—339.

— '68, Reptilien. V. Entwicklungsgeschichtlicher Theil, in: Bronn, Klass. Ordn. Thierreich, V. 6, Abth. 3, p. 1872—1889, tab. 138—170.

— '94, Zur Entwicklungsgeschichte des Selachierkopfes, in: Anat. Anz., V. 9, p. 638—653, 5 Fig.

— '96, Beiträge zur Entwicklungsgeschichte der Selachii, in: Morph. Jahrb., V. 24, p. 209—286, tab. 2—5.

— '97, Beiträge zur Entwicklungsgeschichte der Selachii, ibid. V. 25, p. 250—304, tab. 13—14.

Houssay, F., '90, Etudes d'embryologie sur les Vertébrés, in: Arch. Zool. exp. gén., (sér. 2) V. 8, No. 2, p. 143—244, tab. 10—13. (II. Origine et développement du système nerveux périphérique, p. 178—208.)

Houssay, F., '91, Etudes d'embryologie sur les Vertébrés. IV. Les fentes branchiales auditive, hyo-mandibulaire, spiraculaire et les somites mésoblastiques qui leur correspondent chez l'Axolotl, in: Bull. sc. France Belgique, V. 23, Pt. 1, p. 55—71, tab. 1—3.

Huxley, T. H., '58, The Croonian Lecture. — On the Theory of the Vertebrate Skull, in: Proc. Roy. Soc. London, V. 9, No. 33, p. 381—457, 10 figs.

Kastschenko, N., '88, Zur Entwicklungsgeschichte des Selachierembryos, in: Anat. Anz., Jg. 3, No. 16, p. 445—467.

Killian, C., '91, Zur Metamerie des Selachierkopfes, in: Verh. anat. Ges., V. 5, p. 85—107, 25 Fig.

Kupffer, C., '86, Primäre Metamerie des Neuralrohrs der Vertebraten, in: SB. Akad. Wiss. München, math.-phys. Cl., 1885, p, 469—476.

— '88, Ueber die Entwicklung von Petromyzon Planeri, ibid. V. 18, p. 71—79.

— '90, Die Entwicklung von Petromyzon planeri, in: Arch. mikr. Anat., V. 35, Heft 4, p. 469—558, tab. 27—32.

— '91, Die Entwicklung der Kopfnerven der Vertebraten, in: Verh. anat. Ges., V. 5, p. 22—25.

— '92, Entwicklungsgeschichte des Kopfes, in: Anat. Hefte, Abth. 2, Ergebn. Anat. Entw., V. 2, p. 501—564.

— '93, Die Entwicklung des Kopfes von Acipenser sturio, an Medianschnitten untersucht. Studien zur vergleichenden Entwicklungsgeschichte des Kopfes der Cranioten, Heft 1, München und Leipzig, IV + 95 pp., 9 Taf.

— '94, Die Entwicklung des Kopfes von Ammocoetes Planeri. Studien z. vergl. Entwicklungsgesch. d. Kopfes d. Kranioten, Heft 2, München und Leipzig, 79 pp., 12 Taf.

— '96, Entwicklungsgeschichte des Kopfes, in: Anat. Hefte, Abth. 2, Ergebn. Anat. Entw., V. 5, p. 562—618, 4 Abbild.

Locy, W. A., '94, The optic vesicles of Elasmobranchs and their serial relation to other structures on the cephalic plate, in: Journ. Morph., V. 9, p. 115—122.

— '94a, Metameric segmentation in the medullary folds and embryonic rim, in: Anat. Anz., V. 9, No. 13, p. 393—415, 11 Fig.

— '95, Contribution to the structure and development of the Vertebrate head, in: Journ. Morph., V. 11, No. 3, p. 497—594, tab. 26—30.

— '97, Accessory optic vesicles in the Chick embryo, in: Anat. Anz., V. 14, No. 5, p. 113—124, 9 Fig.

Marshall, A. M., '78, The development of the cranial nerves of the Chick, in: Quart. Journ. micr. Sc., V. 18, No. 69, p. 10—40, tab. 2, 3.

— '81, On the head cavities and associated nerves in Elasmobranchs, ibid. V. 21, p. 72—97, tab. 5, 6.

— '82, The segmental value of the cranial nerves, in: Journ. Anat. Physiol., V. 16, p. 305—354, tab. 10. Also in: Stud. biol. Lab. Owen's College, V. 1, 1886, p. 125—169.

McClure, C. F. W., '89, The primitive segmentation of the Vertebrate brain, in: Zool. Anz., Jg. 12, No. 314, p. 435—438.

— '90, The segmentation of the primitive Vertebrate brain, in: Journ. Morph., V. 4, p. 35—56, tab. 3.

v. Mihalkovics, V., '77, Entwicklungsgeschichte des Gehirns, Leipzig, 203 pp., 7 Taf.

Minot, C. S., '92, Human embryology, New York, XXIII + 815 pp., 463 figs. (p. 604—606.)

— '97, Cephalic homologies. A contribution to the determination of the ancestry of Vertebrates, in: Amer. Natural., V. 31, No. 371, p. 927—943.

— '96, Die frühen Stadien und die Histogenese des Nervensystems, in: Anat. Hefte, Abth. 2, Ergebn. Anat. Ontog., V. 6, p. 687—738.

Neal, H. V., '96, A summary of studies on the segmentation of the nervous system in Squalus acanthias, in: Anat. Anz., V. 12, No. 17, p. 377—391, 6 Fig.

— '98, The segmentation of the nervous system in Squalus acanthias. A contribution to the morphology of the Vertebrate head, in: Bull. Mus. comp. Zool. Harvard Coll., V. XXXI, No. 7, p. 147—294, tab. 1—8, figs. 43.

Oppel, A., '90, Ueber Vorderkopfsomiten und die Kopfhöhle bei Anguis fragilis, in: Arch. mikr. Anat., V. 36, p. 603—627, tab. 30.

Orr, H. B., '87, Contribution to the embryology of the Lizard, in: Journ. Morph., V. 1, p. 311—372, tab. 12—14.

Platt, J. B., '89, Studies on the primitive axial segmentation of the Chick, in: Bull. Mus. comp. Zool. Harvard Coll., V. 17, No. 4, p. 171—190, 2 pls.

— '91, A contribution to the morphology of the Vertebrate head, based on a study of Acanthias vulgaris, in: Journ. Morph., V. 5, p. 79—112, tab. 4—6.

— '91a, Further contribution to the morphology of the Vertebrate head, in: Anat. Anz., V. 6, p. 251—265, 15 Fig.

— '94, Ontogenetische Differenzirung des Ectoderms in Necturus, Studie I, in: Arch. mikr. Anat., V. 43, p. 911—966, tab. 37—42.

— '96, Ontogenetic differentiation of the ectoderm in Necturus. Study II. On the development of the peripheral nervous system, in: Quart. Journ. micr. Sc., V. 38, p. 485—547, tab. 36—38.

Prenant, A., '89, Note sur l'existence des replis médullaires chez l'embryon du porc, in: Bull. Soc. Sc. Nancy, (sér. 2) V. 9, p. 84—93, 1 Pl.

Rabl, C., '85, Bemerkung über die Segmentirung des Hirnes, in: Zool. Anz., Jg. 8, No. 191, p. 192, 193.

— '89, Theorie des Mesoderms, in: Morph. Jahrb., V. 15, p. 113—252, tab. 7—9 u. 9 Fig.

— '92, Ueber die Metamerie des Wirbelthierkopfes, in: Verh. anat. Ges., V. 6, p. 104—135, tab. 2 u. 4 Abbild.

Reighard, Jacob, '90, Development of the Wall-Eyed Pike, Stizostedion vitreum, in: Bull. Michigan Fish Comm., p. 1—66, tab. 1—9, figs. 64.

4

Remak, R., '55, Untersuchungen über die Entwicklung der Wirbelthiere, Berlin, fol. 194 + XXXVIII pp., 12 Taf.

Sedgwick, A., '92, Notes on Elasmobranch development, in: Quart. Journ. micr. Sc., V. 33, p. 559—586, tab. 35.

Sewertzoff, A. N., '95, Die Entwicklung der Occipitalregion der niedern Vertebraten im Zusammenhang mit der Frage über die Metamerie des Kopfes, in: Bull. Soc. imp. Nat. Moscou, Année 1895, p. 186—284, tab. 4 et 5.

— '98, Die Metamerie des Kopfes von Torpedo, in: Anat. Anz., V. 14, No. 10, p. 278—282.

Van Wijhe, J. W., '82, Ueber die Mesodermsegmente und die Entwicklung der Nerven des Selachierkopfes, in: Natuurk. Verh. Akad. Wiss. Amsterdam, V. 22, 50 pp., 5 Taf., 1883. Also separate, Amsterdam 1882, 50 pp., 5 Taf.

— '86, Ueber Somiten und Nerven im Kopfe von Vögel- und Reptilienembryonen, in: Zool. Anz., Jg. 9, No. 237, p. 657—660.

— '86a, Ueber die Kopfsegmente und das Geruchsorgan der Wirbelthiere, ibid. Jg. 9, No. 238, p. 678—682.

— '89, Die Kopfregion der Cranioten beim Amphioxus, nebst Bemerkungen über die Wirbeltheorie des Schädels, in: Anat. Anz., Jg. 4, No. 18, p. 558—566.

— '93, Ueber Amphioxus, ibid. Jg. 8, No. 5, p. 152—172.

Waters, B. H., '91, Some additional points on the primitive segmentation of the Vertebrate brain, in: Zool. Anz., Jg. 14, No. 362, p. 141—144.

— '92, Primitive segmentation of the Vertebrate brain, in: Quart. Journ. micr. Sc., V. 33, p. 457—475, tab. 28.

Wiedersheim, R., '93, Grundriss der vergleichenden Anatomie der Wirbelthiere, 3. Aufl., Jena, XX + 695 pp., 387 Fig., 4 Taf.

Zimmermann, W., '91, Ueber die Metamerie des Wirbelthierkopfes, in: Verh. anat. Ges., V. 5, p. 107—113.

Explanation of Plates.

Plate 28—30.

List of Reference Marks.

1, 2, 3, 4 etc.	metameric segments
a, b, c, d etc.	external grooves that form dividing lines between segments
a', b', c', d' etc.	internal dividing lines between segments
III, IV, V etc.	cranial nerves
opt. n	optic nerves
olf. pt	olfactory pit
au. vs	auditory vesicle
s', s'' etc.	somites
inf	infundibulum
no. co	notochord
gas. ga	Gasserian ganglion
cil. ga	ciliary ganglion
po. com	posterior commissure
r	dorsal groove that divides the primary fore-brain into prosencephalon and thalamencephalon
s	dorsal groove that divides the thalamencephalon into an anterior and a posterior division
e	right epiphysial vesicle
e'	left epiphysial vesicle.

Plate 28.

All figures are of *Salmo purpuratus* (Pallas) except Fig. 9, which represents *Salmo fario* (Mitch.). All are × 60 diameters.

Fig 1. Encephalon of a dissected embryo with 29 somites, 19 days old. Right surface view. Segments 1, 2 and 3 represent the fore-brain, and 4 and 5 the mid-brain. The Anlage of the cerebellum is represented by segment 6.

Fig. 2. Dorsal view of the same encephalon that is represented in Fig. 1. The five segments of the fore- and mid-brain show in this view.

Fig. 3. Encephalon of a dissected embryo with 34 somites, 22 days old. Left surface view. The deep groove *f* forms the anterior limit of the medulla. The groove *c* marks the anterior limit of the mid-brain. The three segments in front of this are very distinct, and constitute the fore-brain. The optic nerve (*opt*) is attached to the ventral portion of segment 2.

Fig. 4. Anterior portion of a living embryo with 33 somites, 22 days old. Left profile view. Segment 6, the cerebellum, and segment 5, the anterior segment of the mid-brain, show very distinctly.

Fig. 5. Anterior portion of a living embryo with 35 somites, 23 days old. Dorsal view. This figure is sketched from two points of view as indicated by the •→ in Fig. 6. The eleven encephalic segments (*1—11*) are separated by transverse grooves that show very distinctly.

Fig. 6. Left profile view of the same embryo that is represented in Fig. 5. The dorsal groove (*f*) has become very distinct. This groove marks the anterior limit of the medulla.

Fig. 7. Anterior portion of a living embryo with 40 somites, 26 days old. Dorsal view, sketched from one point of view. Since the embryos curve ventrally to conform to the spheroid yolk the medulla, in this figure, appears fore-shortened. The three segments (*1*, *2*, *3*) of the fore-brain are very marked on the inner encephalic surface. On this surface the limits of the two segments that form the mid-brain (segments 4 and 5) are also distinct.

Fig. 8. Encephalon of a dissected embryo with 42 somites, 27 days old. Left surface view. The groove *c* marks the anterior limit of the mid-brain. The external surface appears unsegmented. The three segments of the fore-brain (segs. 1, 2 and 3) can still be counted. Segment 2 has become more wedge-shaped as compared with younger stages.

Fig. 9. *Salmo fario.* Anterior portion of a living embryo with 55 somites, 38 days old. Right profile view. The five segments of the fore- and mid-brains (segs. 1—5) show on the inner surface of the brain through the transparent brain wall.

Fig. 10. Right half of the anterior portion of a divided embryo with 31 somites, 20 days old. The internal surface of the encephalon is exposed to view. The groove *c* marks the anterior limit of the mid-brain. The three segments of the fore-brain (segs. 1, 2 and 3) affect the ventral as well as the dorsal zone. The optic stalk (*op.n*) is connected with segment 2. Compare this figure with Fig. 1, external surface of an encephalon one day younger.

Fig. 11. Right half of the anterior portion of a divided embryo with 33 somites, 22 days old. Internal surface of encephalon exposed to view. The groove *f* marks the anterior limit of the medulla. All six segments in front of this groove can be counted. Segment 2 expands to form the infundibulum.

Fig. 12. Left half of the anterior portion of a divided embryo with 37 somites, 24 days old. Internal surface of encephalon exposed to view. Compare this figure with Fig. 8, that shows the external surface of an encephalon 2 days older.

Fig. 13. Right half of the anterior portion of a divided embryo with 39 somites, 26 days old. Internal encephalon surface exposed. Compare this figurewith Fig. 8, which shows the external surface of an encephalon of the same age.

Fig. 14. Left half of the anterior portion of a divided embryo with 44 somites, 28 days old. Internal view of encephalon.

Fig. 15. Left half of the anterior portion of a divided embryo with 54 somites, 36 days old. Internal encephalic surface exposed to view. Segments of the medulla (*7—11*) have passed ventrad. The posterior commissure has appeared at *c*. The transverse groove that formed the dividing line between segments 3 and 4 has disappeared. Secondary folds have formed in the lateral walls of the infundibulum.

Plate 29.

All figures are of the chick embryo. Figures 16—19 are × 27 diameters; the remaining figures (20—33) are × 50 diameters.

Fig. 16. Dorsal view of an embryo with 1 somite, 21 hours old. The neural segments can be traced not only across the wide neural groove, but some distance laterally into the adjacent tissue.

Fig. 17. Dorsal view of an embryo with 2 somites, 22 hours hold. The neural groove is better defined than in the preceding figure.

Fig. 18. Dorsal view of an embryo with 3 somites, 23 hours old. The segments are very pronounced along the neural crests, but can be traced across the base of the neural groove.

Fig. 19. Dorsal view of an embryo with 4 somites, $23^{1}/_{2}$ hours old. The neural groove is about to close. Along the margins of this groove the segments appear more distinctly than they do in younger forms.

Fig. 20. Anterior portion of the neural groove of the same embryo as represented by Fig. 19. Right profile view. The optic evagination covers the first three segments. Transverse external and internal grooves form the dividing lines between adjacent segments.

Fig. 21. Left half of the anterior portion of the divided neural groove of an embryo with 3 somites, 23 hours old. Internal surface exposed to view. This surface is distinctly divided into joints by transverse depressions or constrictions that pass across the divided neural axis.

Fig. 22. Anterior portion of the neural tube of an embryo with $5^{1}/_{2}$ somites, 24 hours old. Dorsal view. *a*, *b*, *c* etc. mark the segmental grooves, and *1*, *2*, *3* etc., the neural segments. The optic evaginations distinctly cover the three anterior segments.

Fig. 23. Right surface view of the same encephalon as represented by Fig. 22. The segments are found to encircle the neural axis. The third segmental groove divides the optic evagination.

Fig. 24. Left half of the same neural tube represented by Figs. 22 and 23. Internal surface exposed to view. The segmentation is especially distinct along the thick dorsal margin. Two transverse ridges

(*c′*, *e′*) have appeared on this surface. They mark the posterior limits, respectively of fore- an mid-brains. The dorsal margins give evidence of three segments in the former (*1*, *2*, *3*) and two segments in the latter (*4*, *5*).

Fig. 25. Encephalon of an embryo with 6 somites, $25^1/_2$ hours old. Dorsal view. The neural groove is closing. *c* and *e* mark the posterior limit of fore- and mid-brains. As in Fig. 24, three segments can be counted in the former (*1*, *2*, *3*) and two in the latter (*4*, *5*).

Fig. 26. Right surface view of the same encephalon as represented by Fig. 25. The second encephalic groove affects the base of the optic evagination. The latter appears divided.

Fig. 27. Left half of the same encephalon represented by Figs. 25 and 26. Internal surface exposed to view. Internal segmental lines appear as transverse ridges (*c′*, *e′*, *g′* etc.). 11 encephalic segments are distinctly present along the thick dorsal margin (*1*—*11*).

Fig. 28. Encephalon of an embryo with 7 somites, 26 hours old. Dorsal view. The three anterior segments can be detected along the dorsal margin. Laterally the optic expansions have obliterated these segments.

Fig. 29. Right surface view of the same encephalon as represented by Fig. 28. In this position all of the neural segments can be seen (*1*—*11*). The component segments of the fore-brain (*1*, *2*, *3*) and of the mid-brain (*4*, *5*) are well defined.

Fig. 30. Encephalon of an embryo with 11 somites, 29 hours old. Dorsal view. The three anterior segments have disappeared. *c* represents the posterior limit of the fore-brain. It will be observed that the optic expansion is now confined to the distal portion of this brain

Fig. 31. Right surface view of the same encephalon as represented in Fig. 30. The dividing groove between the two segments of the mid-brain (*4*, *5*) is about to disappear.

Fig. 32. Encephalon of an embryo with 14 somites, 33 hours old. Dorsal view. The mid-brain now appears unsegmented. Optic evaginations are now connected with the anterior portion of the fore-brain. The dividing line between segments 6 and 7 cannot be seen in this view.

Fig. 33. Right surface view of the same encephalon as represented in Fig. 32. The dividing line between segments 6 and 7, which does not appear in the dorsal view, can be seen in this position. Segment 6 represents the cerebellum. Segment 9 has become wedge-shaped, and in older stages serves as an anatomical landmark.

Fig. 34. Encephalon of an embryo with 16 somites, 36 hours old. Ventral view. Dividing line between segments 6 and 7 is very faint.

Fig. 35. Right surface view of the same encephalon as represented in Fig. 34. Dividing line between segments 6 and 7 can be better seen in this position than in the ventral view (Fig. 34).

Plate 30.

Fig. 36. Encephalon of a chick embryo, 39 hours old. Dorsal view. × 50 diameters. Dividing line between segments 6 and 7 has now become very distinct.

Fig. 37. Encephalon of chick embryo, 43 hours old. Right profile view. × 50 diameters. The six segments of the hind-brain are sharply defined. Segment 6 represents the medulla. Segment 9 is wedge-shaped. The 4th ventricle has appeared, covered by a thin roof.

Fig. 38. Dorsal view of the same encephalon as represented by Fig. 37. × 50 diameters. A dorsal constriction (*r*) has appeared in the primary fore-brain, dividing this region into pros encephalon and thalamencephalon.

Fig. 39. Right profile view of the encephalon of a chick embryo, 47 hours old. × 50 diameters. Limits of the neural segments in the medulla are sharply defined. The dorsal constriction (*r*) divides the primary fore-brain as described in Fig. 38.

Fig. 40. Encephalon of a chick embryo, 50 hours old. Right profile view. × 36 diameters. A dorsal groove (*s*) has appeared, dividing the thalamencephalon. These large anterior divisions are very different, however, from the neural segments of the medulla (*6—11*). Failure to recognize this has led to confusion.

Fig. 41. Encephalon of a chick embryo, 80 hours old. Right surface view. × 19 diameters. The segments of the medulla are about to disappear. Segment 6 represents the cerebellum and forms the anterior boundary of the 4th ventricle. The portion between *c* and *r* represents the thalamencephalon and is divided by the groove *s* as represented in Fig. 40. The portion in front of *r* represents the prosencephalon. A median furrow in the dorsal region has divided this into the right and the left lobes of the cerebrum.

Fig. 42. Parasagittal section through the anterior portion of *Salmo purpuratus*, 22 days old. × 60 diameters. Segment 6 represents the cerebellum. Five segments (*1—5*) can be counted in front of this. Segments 1, 2, 3 represent the fore-brain, and segments 4 and 5 represent the mid-brain.

Fig. 43. Horizontal section through the head of *S. purpuratus*, 26 days old. × 60 diameters. The section divides the right eye, but passes dorsal to the left eye. It passes through the dorsal encephalic region, therefore segment 2 is narrow and segment 3 is broad. Compare this with Fig. 13, Plate 1.

Fig. 44. Horizontal section through the anterior portion of a chick embryo with 4 somites, $23^{1}/_{2}$ hours old, with open neural groove. Eleven neural segments are present (*1—11*). The dividing lines between these segments appear as external and internal transverse grooves. Compare this with Figs. 19 and 20 representing an embryo of the same age as Fig. 44.

Fig. 45. Horizontal section through the right wall of the medulla of a chick embryo with 14 somites, 33 hours old. × 275 diameters.

The internal ridge just opposite the external groove *g* has at its apex a groove *g'*. These grooves mark the dividing line between neural segments 7 and 8. Compare this with Fig. 46.

Fig. 46. Horizontal section through the left wall of the medulla of *S. purpuratus*, 22 days old. × 275 diameters. The external and internal grooves (*g* and *g'*), as in Fig. 45, mark the dividing line between neural segments 7 and 8.

Fig. 47. Transverse section through the head of *S. purpuratus*, 31 days old. The section passes through the region of the mid-brain and shows on the left side the oculomotor nerve (*III*) and its connection with the brain.

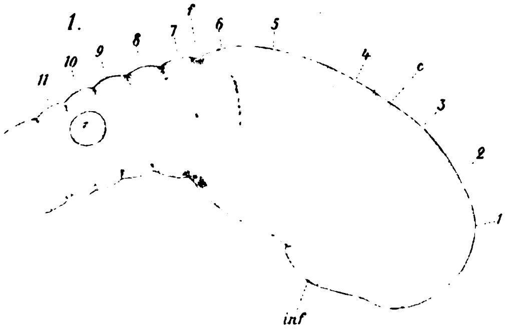
Fig. 48. Horizontal section through the cerebellum (segment 6) and adjacent segments of *S. purpuratus*, 23 days old. The right side only is represented, and shows the connection of the anterior root of the right trigeminal nerve with the crest of the cerebellum and the Gasserian ganglion.

Fig. 49. Horizontal section through the head of *S. purpuratus*, 31 days old. On the left side the section shows the union of the fifth pair of cranial nerves with segment 7 and the seventh and eighth pair with segment 9.

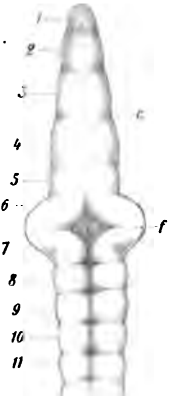
Fig. 50. Horizontal section through the head of a chick embryo, 40 hours old. The figure represents only the right side, and shows the union of the fifth pair of nerves with the posterior portion of segment 7, the union of the seventh and eighth pair with the posterior portion of segment 9, and the union of the ninth pair with segment 11.

Frommannsche Buchdruckerei (Hermann Pohle) in Jena.

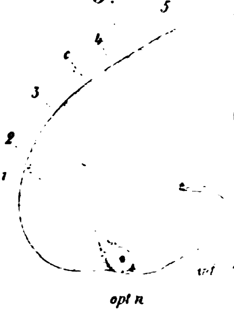
1.



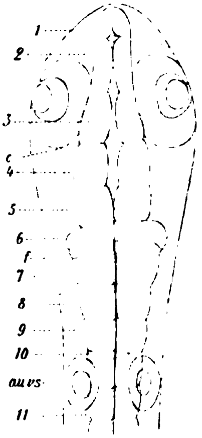
2.



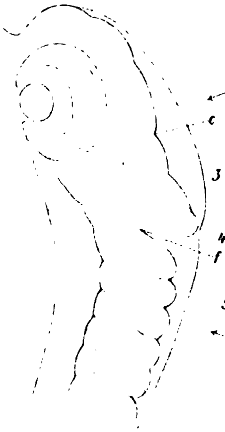
3.



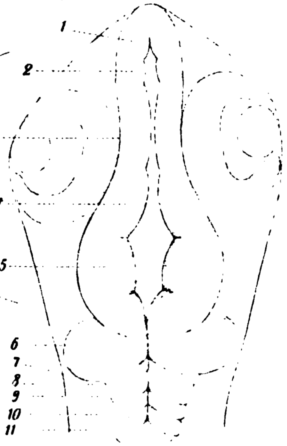
5.



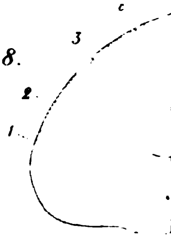
6.



7.

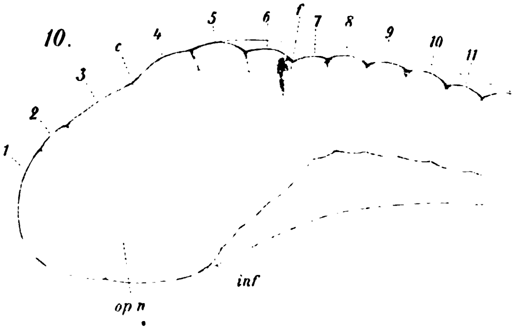


8.

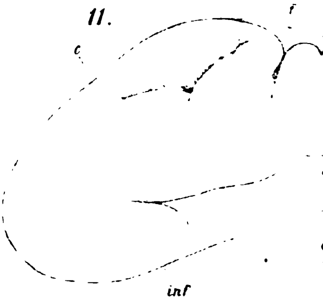


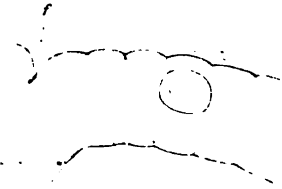
14.

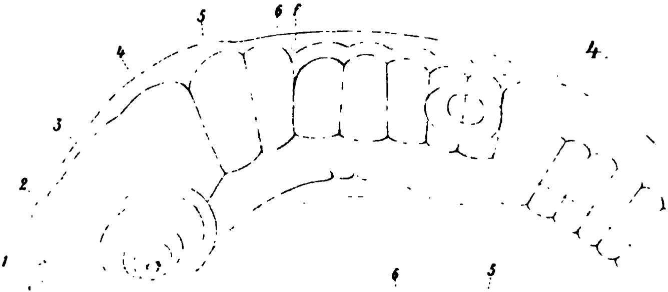
10.

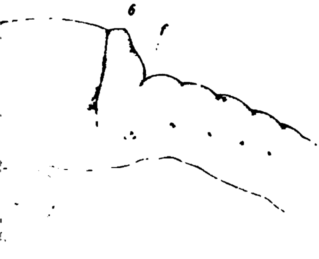


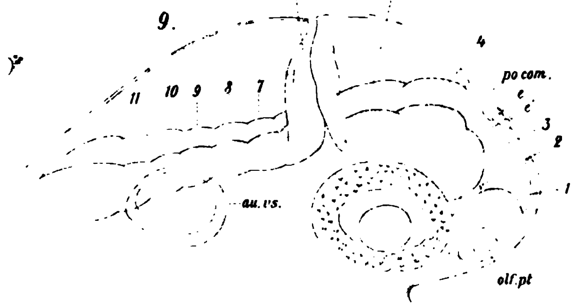
11.

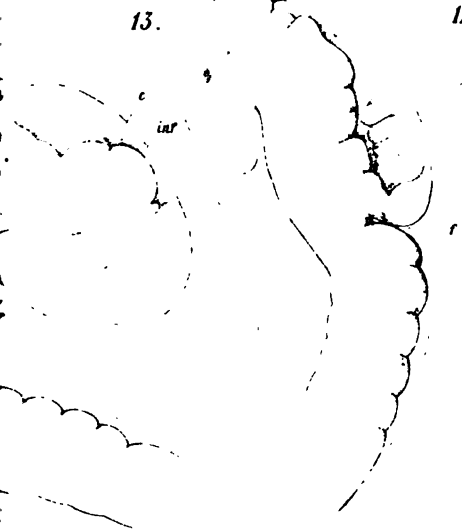


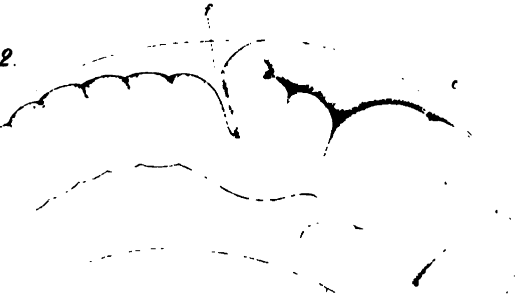


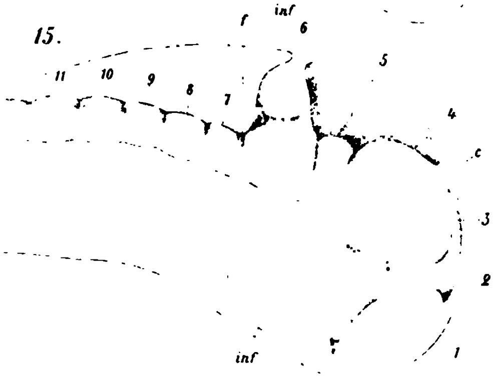

4.




9.

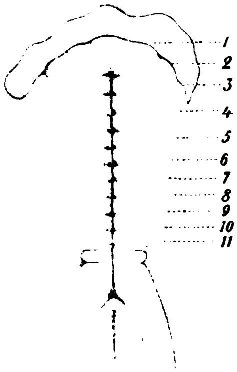

13.


12.

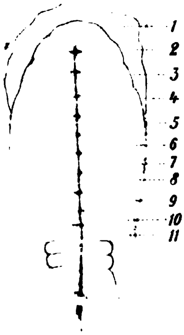

15.

lav Fischer

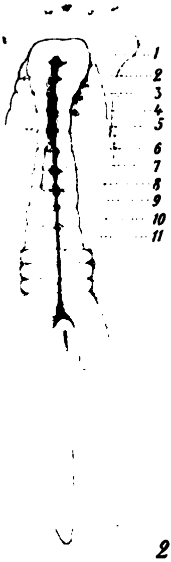
16.



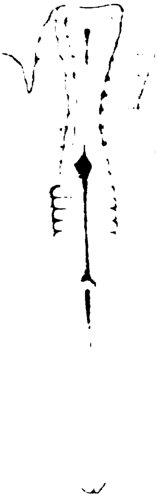
17.



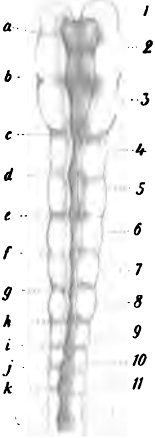
18.



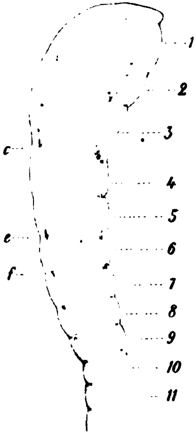
19.



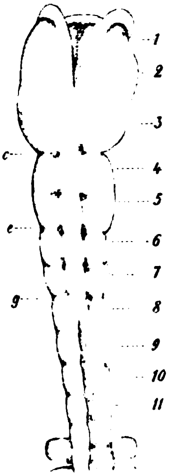
22



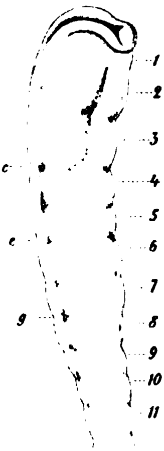
23.



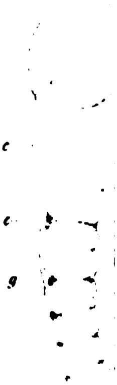
25.



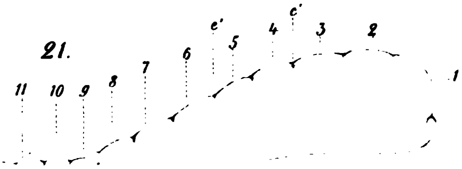
26.



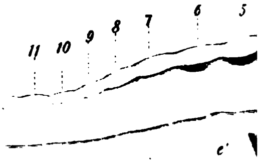
31.



21.

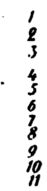


24.

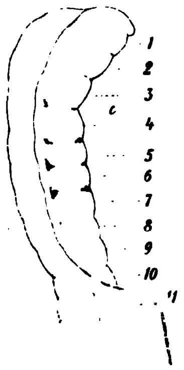


Gust

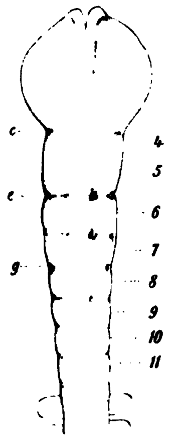
Taf. II.



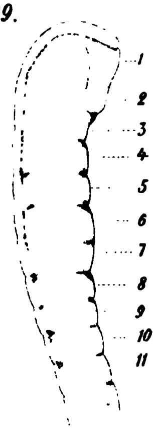
20.



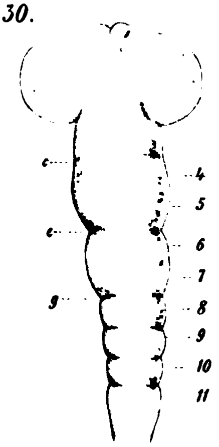
28.



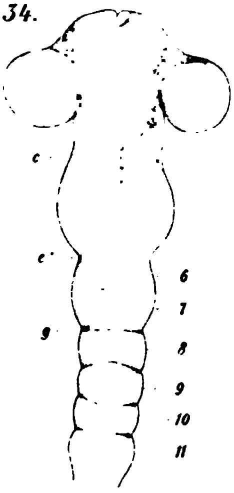
29.



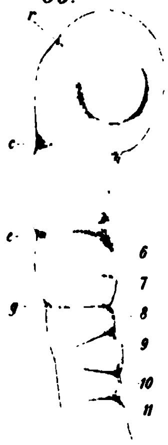
30.



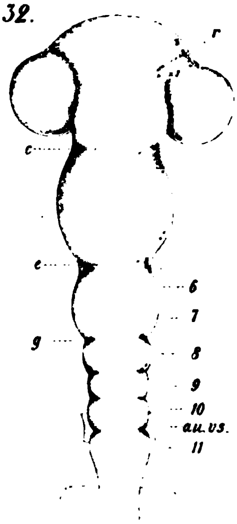
34.



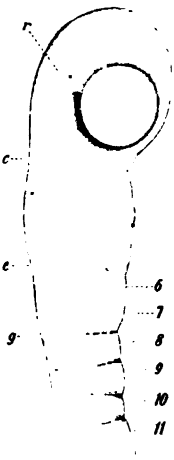
35.

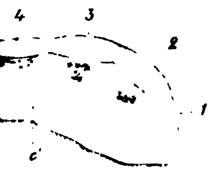


32.

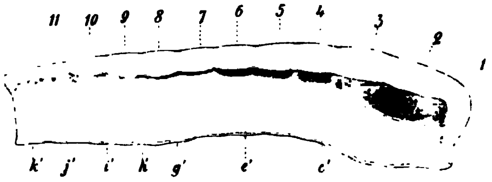


33.



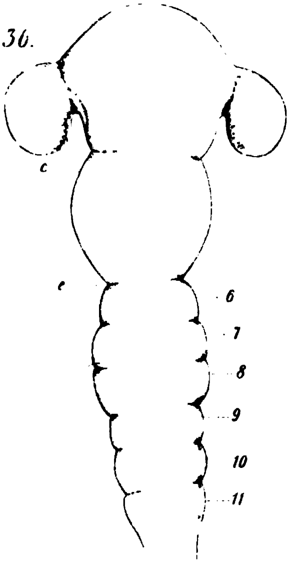


27.

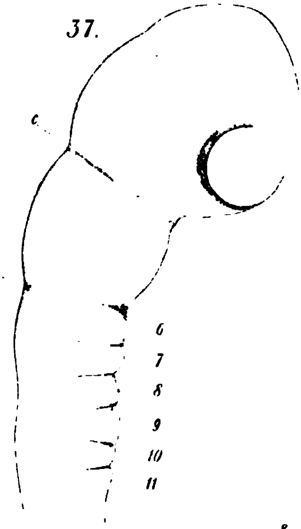


Fischer

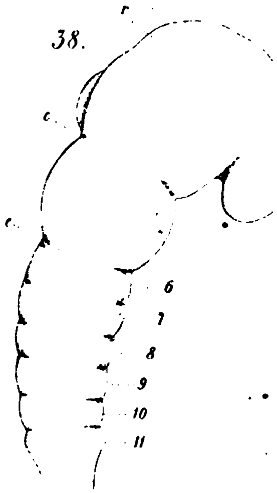
36.



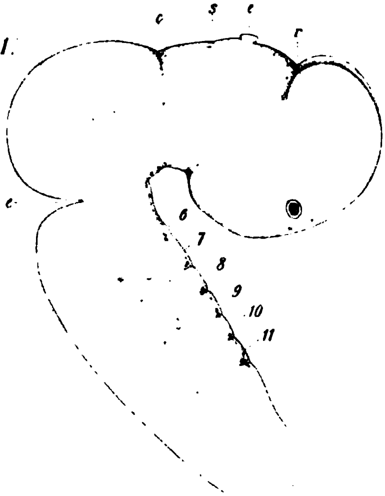
37.



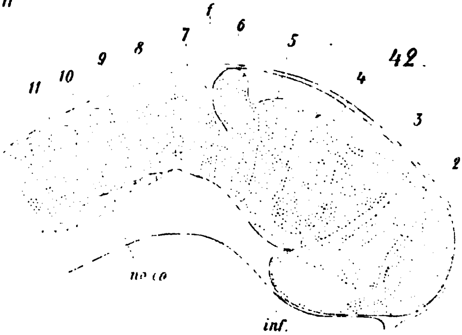
38.



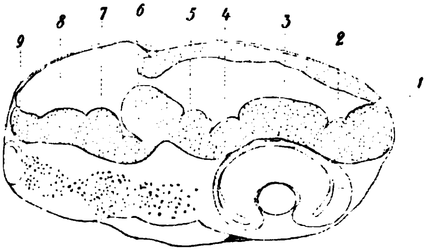
41.



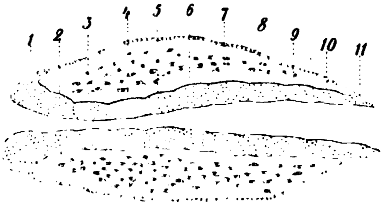
42.



43.



44.



48.